A review of mating behavior in slugs of the genus *Deroceras* (Pulmonata: Agriolimacidae)*

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Abstract: The genus *Deroceras* Rafinesque, 1820 (the largest genus of terrestrial slugs) shows a high diversity of penis morphologies and mating behaviors. The function of most of the appending external and internal penial structures, some of them truly bizarre, is largely unknown. This paper reviews mating behavior and reproduction, based on data on 16 species from the literature and from unpublished observations. I analyze patterns common to all *Deroceras* species and differences among species. The general mating pattern consists of a long courtship with mutual stroking with a sarcobelum, a sudden penis eversion, and external sperm exchange (copulation). I distinguish also precourtship and withdrawal phases. Sperm exchange is usually very quick but, in a few species, occupies a considerable proportion of the total mating duration. Mutual sperm exchange is the rule. Species differences involve the durations of certain mating phases, presence and nature of initial trail following, nature and intensity of stroking (including the degree of contact with the sarcobelum), aggressiveness of courtship behavior, and the timing of the penial gland eversion. I hypothesize that the radiation of mating behaviors and associated structures has been driven by an arms race resulting from conflicting interests of mating partners over sperm donation and use. This could also have increased the rate of speciation in *Deroceras*. There are indications of the presence of sperm competition and conflicting interests between mating partners: individuals mate repeatedly, can store and digest sperm, and simultaneously use sperm from different mating partners for fertilization. Some details of mating behavior also indicate conflict. The timing of the penial gland eversion after sperm exchange suggests a manipulation akin to the role of love darts in helicid snails. Finally, some recommendations for studying mating behavior in *Deroceras* are given.

Key words: courtship, genital morphology, partner manipulation, sexual conflict, simultaneous hermaphrodite

Deroceras Rafinesque, 1820 is the largest genus of terrestrial slugs (over 100 known species), and comprises the major part of the slug family Agriolimacidae (Wiktor 2000). It is Holarctic with most species restricted to the Palaearctic, although a few synanthropic species have been introduced to most other continents. The widespread pest species have been comparatively well studied. However, there are many species with apparently small geographic ranges, and for a number of species not much more than the morphology and type locality is known. There is no well-supported phylogeny of *Deroceras* available except for the separation of six species into the subgenus *Liolytopelte* Simroth, 1901.

Deroceras slugs are externally rather uniform (each species has some externally identical congeners), and most of the internal anatomy also varies very little among species. Almost the only species-specific characters are provided by the penial morphology: there is a wide variety of appending and internal structures (side pockets, glands, folds, pilasters, etc.), but their functions are largely unknown.

The diversity of penial morphologies is accompanied by a diversity of mating behaviors, and even sibling species can differ considerably (Gerhardt 1935, Reise 1995, 2001, Wiktor 2000). I review here the mating behavior of *Deroceras* and indicate which patterns are consistent in all species and which vary among or within species. The elaborate mating behavior and the diversity of penial structures, including rather extravagant and bizarre structures, caused Reise (2001) to hypothesize that the diversity of mating behaviors and associated genital structures is driven by an evolutionary arms race between male and female functions in these simultaneous hermaphrodites.

The background to this hypothesis is that at least some species of *Deroceras* are able to self-fertilize and/or to mate repeatedly (Rymzhanov and Schileyko 1991, Rymzhanov 1994, Reise 1996, 1997, 2001, Lebovitz 1998, Wiktor 2000 and references he cites on p. 375). Moreover, they may simultaneously use sperm from different mating partners for fertilization of a single clutch (H. Reise, B. Zimdars, M. Scheibe, J. Sauer, and C. Matthieu, unpubl. obs. on *Deroceras panormitanum* (Lessona and Pollonera, 1882)). A receiver might thus not use the donor's sperm and instead use sperm from another (earlier or later) donor or its own sperm to fertilize its eggs (unused ejaculates may be digested in the bursa copulatrix). It is even possible that individuals try not to donate sperm in some matings if it would be better to invest the ejaculate in a higher-quality partner or if there are indications that this partner would only digest the ejaculate (Leonard 1991, Michiels 1998). A sexual conflict could arise if partners attempt to avoid one of the sexual roles (male or

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female) or if sperm donors can manipulate their partners to use this batch of donated sperm to fertilize more eggs. Counter-adaptations would lead to an evolutionary arms race; this might drive rapid diversification and the development of bizarre genital structures and mating behaviors. Evolutionary arms races driven by sexual conflict have been convincingly shown in gonochorists (Rice 2000), and Leonard (1990, 2006), Michiels (1998), and Michiels and Koene (2006) have proposed that sexual conflict may also be strong in simultaneous hermaphrodites. Convincing evidence for an arms race between sperm-donating and sperm-receiving functions in simultaneous hermaphrodites comes from a comparative analysis of love-dart shooting and receiving organs in helicid snails (Koene and Schulenburg 2005). There are also indications of intraspecific coevolution of male and female reproductive traits in the terrestrial snail *Arianta arbustorum* (Linnaeus, 1758) (Beese *et al.* 2006).

My review is based on data on mating behavior from 16 species (Table 1). These data include my own published and unpublished observations as well as descriptions by others. The published descriptions vary considerably in quality. Some are based on single or very few chance observations in the field and provide little information. Some others do not specify sample sizes. My own unpublished observations (and those of M. Benke and I. Schulze) cited in this paper are based on laboratory observations of the mating behavior of wild-collected or laboratory-bred individuals. Animals were kept isolated for a few days prior to being put together and then kept under at least periodic observation for a few hours until they did or did not start to mate; thus my observations often include early precourtship behavior. In all species at least some matings were video-recorded.

Comparisons are hampered by inconsistent or unclear definitions of mating phases (see section on general mating pattern) and by uncertain species identities; these have also led to misunderstandings between authors. A particularly good example is Carrick's (1938) description of the mating behavior of *Deroceras agreste* (Linnaeus, 1758) (probably what we

now know as *D. reticulatum* (Müller, 1774), see below), based on one field observation in Scotland. The author seems to have misunderstood the sarcobelum as the penis, and he reported that it was inserted into the partner's genital aperture. Consequently, he interpreted the entire courtship as copulation and saw discrepancies with the copulation time given for this species by Taylor (1902-1907). He may possibly have been confused by Heath's (1916) description of the mating behavior of *Ariolimax californicus* (Gould *in* A. Binney, 1851), an arionid slug with penis intromission. The genus *Deroceras* was called *Agriolimax* Mörch, 1865 at this time, and a misspelling in the reference list implies that he confused the similar generic names and thought to see what he expected.

The commonest example of uncertain species identity is that in older papers *Deroceras reticulatum* was usually not distinguished from *D. agreste*, so that it is unclear which

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Table 1. Sources of data on mating in *Deroceras*. (*: species identity uncertain).

Subgenus *Deroceras* s.s.

D. agreste (Linnaeus, 1758)	Gerhardt 1933, 1934*, H. Reise, unpubl. obs. (1 mating)
D. fatrense Mácha, 1981	Reise, unpubl. obs. (≥12 matings)
D. gorgonium Wiktor *et al.*, 1994	Reise *et al.* 2007
D. laeve (Müller, 1774)	Karlin and Bacon 1961*, Rymzhanov 1994*, Barker 1999*
D. lombricoides (Morelet, 1845)*	Simroth 1891, Castillejo *et al.* 1989
D. nitidum (Morelet, 1845)	Castillejo *et al.* 1989
D. panormitanum (Lessona and Pollonera, 1882)	Gerhardt 1939, Quick 1960, Webb 1961, 1965, Barker 1999, Reise and Hutchinson 2001b, Benke *et al.* 2005, Benke 2006, H. Reise, M. Scheibe, J. Sauer and C. Matthieu, unpubl. obs. (≥60 complete matings)
D. planarioides (Simroth, 1910)	Gerhardt 1939*
D. praecox Wiktor, 1966	Reise 1995, unpubl. obs. (≥29 matings)
D. rethimnonensis de Winter and Butot, 1986	Wiktor 1994
D. reticulatum (Müller, 1774)	Simroth 1885, Gerhardt 1933*, 1934, Wiktor 1960, Karlin and Bacon 1961, Webb 1961, 1965, Nicholas 1984, Barker 1999, H. Reise, unpubl. obs. (≥2 matings)
D. rodnae Grossu and Lupu, 1965	Reise 1995, 1997, unpubl. obs. (≥33 matings)
D. sturanyi (Simroth, 1894)	Gerhardt 1936*—as "*D. laeve*", Kosińska 1980, Rymzhanov 1994, H. Reise and C. Natusch, unpubl. obs. (6 matings)
D. turcicum (Simroth, 1894)	Gerhardt 1935*—as "*Deroceras* aff. *turcicum*", H. Reise, unpubl. obs. (≥7 matings)

Subgenus *Liolytopelte*

D. bureschi (Wagner, 1934)	Wiktor 1983, 2000
D. caucasicum (Simroth, 1901)	Rymzhanov and Schileyko 1991

species were observed (Wiktor 2000). Gerhardt's (1933, 1934, 1936, 1939) valuable descriptions of the mating behavior of several *Deroceras* species were hampered by uncertain species determinations (Gerhardt 1934, 1939, Wiktor 1960). In 1933, he published descriptions for "*Agriolimax agrestis*" and "*Agriolimax laevis*", but later corrected their identities to "*Deroceras reticulatum*" and "*Deroceras agreste*", respectively (Gerhardt 1934), which is how I will refer to his 1933 descriptions. Then in 1936 Gerhardt described the mating behavior of a species that he thought to be the real *Deroceras laeve* (Müller, 1774). However, he later expressed some uncertainty about the species identity (Gerhardt 1939). It seems probable that he was indeed wrong again: all details that Gerhardt (1936) provided about his *D. laeve*—time of occurrence, body color, sarcobelum shape and its use during courtship, bulbous shape of everted penial mass, and unusually long copulation—fit very well with the externally hard-to-distinguish *D. sturanyi* (Simroth, 1894), a species of which malacologists were hardly aware at that time and with which *D. laeve* has often been confused (Quick 1960). Later descriptions of matings of *D. laeve* with which one might compare are sparse: Karlin and Bacon (1961) repeated Gerhardt's (1936) statement that its courtship is similar to that of *D. reticulatum* but stress that the partners have less intimate contact. However, they do not mention copulation, which they probably would have done had they observed it. Barker (1999) just repeated information provided by Gerhardt (1936) and Karlin and Bacon (1961), so one has to wonder to what extent Barker observed the mating of *D. laeve*. Rymzhanov's (1994) description of the mating behavior of *D. laeve* from Kazakhstan differs in almost every aspect from the earlier papers. The origin that Rymzhanov (1994) proposed for the aphallic individuals in his population (apophallation) differs from what we know of their origin in Europe, so Kazakh *D. laeve* may well be a distinct species. Thus, although four publications claim to describe the mating behavior of *D. laeve*, there are no reliable data. In this paper I will consider the species studied by Gerhardt (1936) as *D. sturanyi* and refer to the one described by Rymzhanov (1994) as "Kazakh *D. laeve*". The papers of Karlin and Bacon (1961) and Barker (1999) will be assumed to pertain to *D. laeve*, because *D. sturanyi* is unknown in North America and New Zealand, but this should be viewed as provisional.

I do not include other genera of the Agriolimacidae because at least some are considerably different in their genital anatomy and thus possibly also in their mating behavior. Besides, almost nothing is known about them. The only published description of mating behavior in another agriolimacid genus concerns a species of *Furcopenis* Castillejo and Wiktor, 1983 (Rodríguez *et al.* 1989), morphologically the most similar genus to *Deroceras*, of which it had formerly been classified as a subgenus.

Casual observations suggest that mating often occurs during early morning, but no one has carried out systematic observations throughout 24 hours, so I do not attempt to review this aspect of mating behaviour. Mating slugs are often observed in the open, but again there are no systematic observations of what proportion of matings in the wild are hidden, for instance under leaves.

GENITAL MORPHOLOGY

There are discrepancies in how to describe the relative position of parts of molluscan genitalia. Sometimes, the parts further away from the genital pore are called "proximal" (*e.g.*, Castillejo *et al.* 1989, Rymzhanov 1994, Reise 1997, 2001, Hausdorf 1998, Barker 1999, Reise and Hutchinson 2001a) and sometimes "distal" (*e.g.*, Quick 1960, Webb 1965, Nicholas 1984, Backeljau and De Bruyn 1990, Reise 1995). Some authors use "anterior" and "posterior", "basal" and "terminal", or other terms relating to the approximate positions of the organs in the animal at rest and their orientations (*e.g.*, Mead 1943, Webb 1961, Sirgel 1973, Rähle 1998, Tompa 1984, Wiktor 2000). However, as not all sections of the genital tract are orientated anterior-posterior in animals at rest, I will use the terms proximal and distal and apply the first definition, which is that used in medicine: parts of the genitalia nearer to the genital pore are further away from the body centre (when not everted) and thus distal. Parts further away from the genital pore, and thus nearer to the body centre, are proximal (Fig. 1).

In the genital tract of *Deroceras* (Fig. 1), the penis has a more or less sac-like shape, but can consist of one or more chambers and may have side pockets and diverse appendages. In at least one species, *D. laeve*, the penis is often
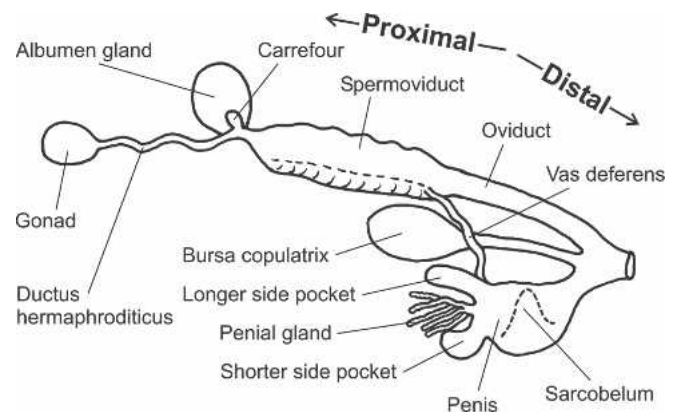

Figure 1. Schematic genital tract of *Deroceras panormitanum* [after fig. 5.1 in South (1992)].

reduced (hemiphallic) or entirely lacking (aphallic) (Simroth 1884, Wiktor 1973, 2000, Tompa 1984).

Most species have a more-or-less finger-like penial gland appending somewhere near the proximal end of the penis. This is also called the trifid or penial appendage (*e.g.*, Quick 1960, Runham and Hunter 1970, Runham 1978) or flagellum (*e.g.*, Simroth 1885, Gerhardt 1933, 1935, Wiktor 1960, Webb 1961); it may or may not be homologous to the flagellum of helicid snails (Sirgel 1973, Nicholas 1984, Hausdorf 1998). The name "penial gland" seems justified because there are indications for secretory activity (Sirgel 1973, Nicholas 1984, Benke et al. 2005, Benke 2006). Interspecifically, the penial gland varies widely in size, can be branched or unbranched, and lobed or smooth (Fig. 2). In some species, particularly *Deroceras gorgonium* Wiktor *et al.*, 1994 (Fig. 2F), it is extremely large and tree-like. The number of branches can vary intraspecifically (Wiktor 2000, Benke 2006).

The lumen of the penis also contains diverse structures. The most important is the sarcobelum (or stimulator; "Reizkörper" of earlier German authors), located in the distal, swollen part of the penis. It is a conical or tongue-like structure, solid but with a central blood sinus, and consists of muscle, glandular, and connective tissue cells in a collagen matrix (Nicholas 1984). The sarcobelum plays an important role during courtship when it is pushed outside the genital orifice by the eversion of the distal part of the penis (the sarcobelum itself does not evaginate). Its surface has longitudinal ridges with a strongly ciliated epithelium, and there are gland cells in the sarcobelum and the surrounding inner penial wall (Sirgel 1973, Els 1978, Nicholas 1984). This and its use during courtship suggest that this organ transfers secretions onto the mating partner. Shape and size of the sarcobelum vary considerably among species (Fig. 3). Species of the subgenus *Liolytopelte* have a calcareous plate at the base of the sarcobelum (Fig. 3D).

The walls of other penial protuberances have also been reported to contain glands (Wiktor 2000). However, the function of these and most other penial structures is largely unknown.

The sac-like bursa copulatrix (also called "spermatheca") opens, via the bursa trunk, into the genital atrium (Nicholas 1984) or base of the penis (Hausdorf 1998, Wiktor 2000). It is a lytic organ and digests excess sperm as well as some other secretions (Nicholas 1984, Tompa 1984), probably including other components of ejaculates.

GENERAL MATING PATTERN

The mating pattern of *Deroceras* consists of four main phases (Fig. 4).

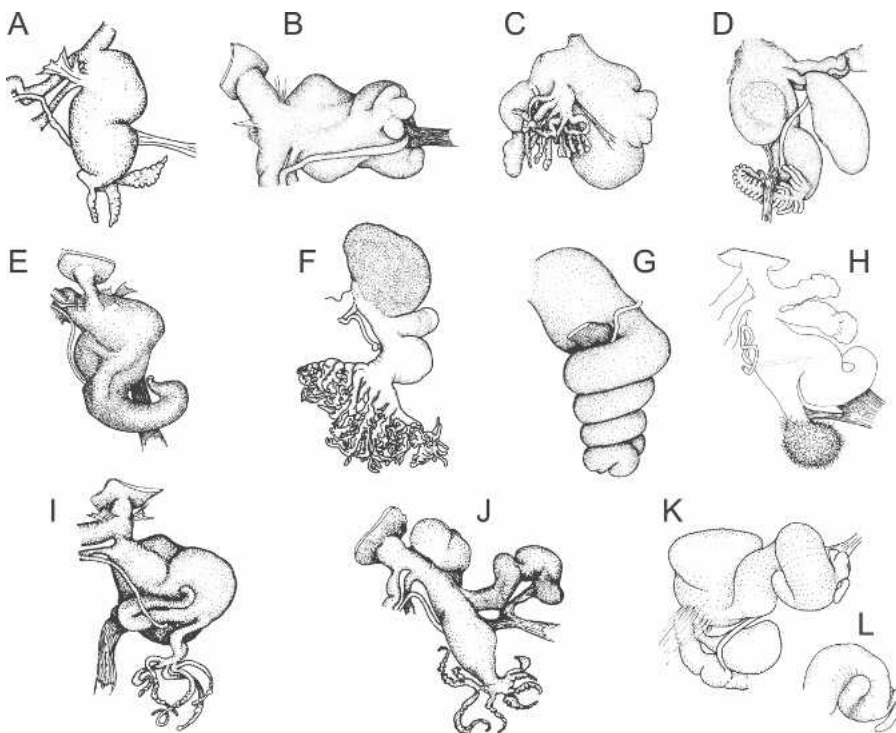(i) Precourtship phase: the partners encounter and investigate each other.

Figure 2. Penis diversity in *Deroceras*. A, *D. reticulatum*. B, *D. minoicum* Wiktor *et al.*, 1994. C, *D. ikaria* Reischütz, 1983. D, *D. christae* Rähle, 1998. E, *D. adolphi* Wiktor, 1998. F. *D. gorgonium*. G, *D. helicoidale*. H, *D. glandulosum* (Simroth, 1904). I, *D. giustianum* Wiktor, 1998. J, *D. oertzeni* (Simroth, 1889). K, L, *D. praecox*. L, pocket at proximal end of penis—different perspective of same specimen as K. Sources of drawings: A, H, Wiktor 2000; B, Wiktor *et al.* 1994; C, J, Wiktor 2001; D, G, Rähle 1998; E, I, Wiktor 1998; F, Reise *et al.* 2007; K, L, Reise and Hutchinson 2001a. Reproduced by permission of the Museum and Institute of Zoology of the Polish Academy of Sciences (A, D, H), the Museum of Zoology Dresden (B, G, E, I), the Natural History Museum of Crete (C, J), Springer (F), The Association of Polish Malacologists (K, L).
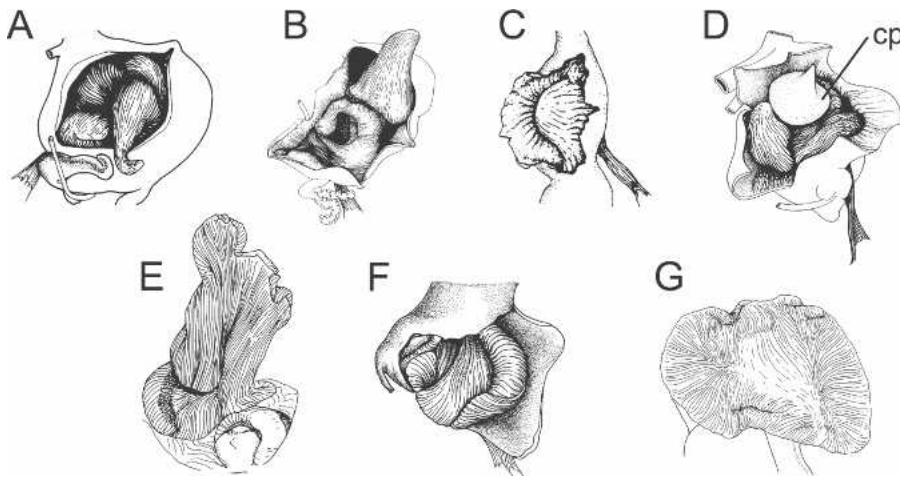
Figure 3. Variability of sarcobelum shapes in *Deroceras*. Conical sarcobelum: A, *D. giustianum* Wiktor, 1998. B, *D. rethimnonensis*. C, *D. laeve*. With calcareous plate at base of sarcobelum (cp): D, *D. (Liolytopelte) caucasicum*. Flat sarcobelum: E, *D. rodnae* from SE Poland. F, *D. subagreste* (Simroth, 1892). G, *D. bistimulatum* Wiktor, 2000 (sarcobelum consisting of two lobes; here protruded through the genital opening). Sources of drawings: A, Wiktor, 1998; B, Wiktor 2001; C, D, F, G, Wiktor 2000. Reproduced by permission of the Museum of Zoology Dresden (A), the Natural History Museum of Crete (B), the Museum and Institute of Zoology of the Polish Academy of Sciences (C, D, F, G).
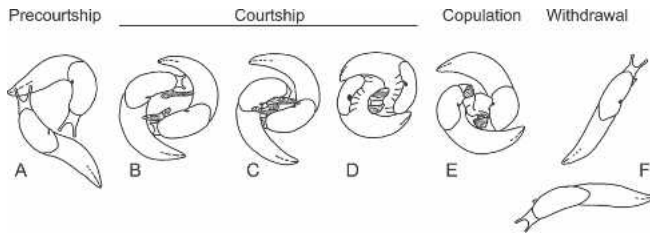

Figure 4. General mating pattern of *Deroceras* [after Reise (1995)].

(ii) Courtship phase: both partners have their sarcobelum protruded from the genital opening and assume a position with their genital pores facing each other, forming a circle or yin-yang configuration.

(iii) Copulation phase: the slugs evert their penes, entwine them, and mutually transfer the ejaculates from penis to penis (there is no intromission).

(iv) Withdrawal phase: the penes are retracted together with the attached sperm masses.

I consider the beginning of precourtship as the moment when two slugs start to show clear signs of interest: investigating each other with tentacles or mouth, circling, or trail following. I refrain from the synonymous term "recognition phase" (*e.g.,* Reise 1995) because this implies too restricted a function. I define courtship as starting when both partners have everted their sarcobela. The separation of precourtship and courtship seems reasonable in the majority of species in which the behaviors during these two phases clearly differ. However, there are species with less clear-cut separations: for example, in *Deroceras gorgonium* the partners may not evert their sarcobela at roughly the same time and they may retract them repeatedly (Reise *et al.* 2007). For this reason, and to enable comparisons with other authors, I also use the

term "precopulatory phase", meaning precourtship + courtship. Barker (1999) occasionally used this term without clearly defining it.

I define the beginning of copulation as when penis eversion starts (excluding the earlier partial eversion of the distal penis that protrudes the sarcobelum). Copulation ends and withdrawal starts when the genitalia lose contact with the partners. Withdrawal ends when the genitalia are fully retracted into the body (but not necessarily into the original position within the body, which can take much longer: Webb 1961, Nicholas 1984). Behavior related to mating may continue after withdrawal: during mating, particularly during copulation, the partners secrete abundant mucus, which covers the mating substratum (Simroth 1885, Gerhardt 1933, Wiktor 1960, 2000, Karlin and Bacon 1961, Kosińska 1980, Reise 1995), and this is often eaten by one or both partners after withdrawal (Kosińska 1980, Wiktor 2000). Also, slugs have been observed to lick off penial gland secretion received during copulation (see copulation section).

There are some discrepancies in the distinction of mating phases and their nomenclature by different authors. This complicates interspecific comparisons. For example, Castillejo *et al.* (1989) called the entire mating (except precourtship) "copulation", whereas Rymzhanov and Schileyko (1991) called it (including precourtship) "courtship", as apparently did Barker (1999). At one point in his paper Rymzhanov (1994) applied a Russian term for "mating play" to the entire mating, as do Rymzhanov and Schileyko (1991) but at another point he restricted this term to only the precopulation phase.

Often, particularly in older publications, mating is divided into only two phases: the behavior before copulation and the copulation. The first part has been called the nuptial dance (Wiktor, 1960, Pilsbry 1948), Vorspiel (*i.e.,* foreplay: Simroth 1885, 1891, Gerhardt 1933, 1935, 1939, 1940) or

courtship (Webb 1961, Tompa 1984). It is often unclear whether the descriptions of courtship include only courtship behavior in my strict sense or also precourtship. Often little attention has been paid to this precourtship phase, either because the behavior was not recognized as early mating, or because observations started only at courtship (usually the case with field observations). However, in some cases precourtship was clearly considered as a first part of courtship, as by Karlin and Bacon (1961) who used the term "positional movements", or it was distinguished as a separate "recognition" phase (Kosińska 1980, Reise 1995, 1997, Wiktor 2000). This is then followed by the "stimulation phase", "mating dance" or "excitatory movements" (courtship in my strict sense; Karlin and Bacon 1961, Wiktor 2000) or "courtship" and "pre-copulation" (Kosińska 1980). Rymzhanov (1994) distinguished three different precopulatory phases: recognition (for the first, short mutual investigations), following (for apparent trail-following behavior, but including some time when sarcobela are already everted), and circling.

The copulation, also called coition (Karlin and Bacon 1961, Webb 1961) or Begattung (Gerhardt 1933, 1936), has also not been clearly defined. While almost all authors seem to agree that copulation starts when the major parts of the penes begin eversion and entwine, I know of no publication clearly defining the ending of the copulation and withdrawal phases. In only a few papers has withdrawal been distinguished as a phase (Reise 1995, 1997, Wiktor 2000); it was called "postcopulation" in *Deroceras sturanyi* and Kazakh *D. laeve* (Kosińska 1980, Rymzhanov 1994).

Matings are sometimes broken off, primarily during the precourtship or early courtship phases (Kosińska 1980, Rymzhanov 1994, Reise 1995, Wiktor 2000, M. Benke, pers. comm.); this suggests that the function of the long courtship is not mate choice but there could be an influence of courtship on sperm exchange or on its subsequent use. A retreat from courtship into precourtship behavior is also possible; that is, one or both slugs retract their sarcobelum but evert it again later. This seems to happen to different degrees in different species (see comments above on *Deroceras gorgonium*).

Sometimes more than two slugs are involved in precourtship and/or courtship (Simroth 1885, Gerhardt 1933, 1935, Wiktor 1960, Karlin and Bacon 1961, Kosińska 1980, Rymzhanov and Schileyko 1991, Reise 1995, unpubl. obs.). Either all slugs (usually three, but Rymzhanov and Schileyko [1991] saw up to seven) start mating behavior more or less simultaneously, or one individual is attracted by a mating couple. Rymzhanov and Schileyko (1991) stated that the precourtship phase is omitted in such cases, and that participating individuals had usually mated already, but Reise *et al.* (2007) observed trail following with alternating participation. The participation of additional individuals in a

courtship can lead to apparent confusion and seems to delay the mating process (Rymzhanov and Schileyko 1991, H. Reise, unpubl. obs.). Never were more than two slugs observed to be involved in a copulation (Karlin and Bacon 1961, H. Reise, unpubl. obs.); either courtship was broken off by all slugs (and two slugs might start again later) or one partner would leave earlier (H. Reise, unpubl. obs.) or would not participate in copulation (Simroth 1885).

Individuals will usually mate again after a few days (H. Reise, unpubl. obs.). However, Rymzhanov and Schileyko (1991) and Rymzhanov (1994) observed that *Deroceras sturanyi* would mate only twice, and that in *D. caucasicum* (Simroth, 1901) the third and fourth courtships would not lead to copulation. This does not agree with my own observations on various other species of *Deroceras*; this discrepancy might have to do with species differences or with methodology. I found that animals will remate in the laboratory more than twice if isolated for several days between matings, but they stop showing interest in mating at a later stage of adulthood, irrespective of whether they have mated already or not. Rymzhanov and Schileyko (1991) used field-collected specimens so they did not know the slugs' ages and possibly not their full mating histories.

TIMING

Even allowing for uncertain or differing definitions of each phase in different publications, species clearly differ considerably in the absolute and relative durations of mating phases (Table 2). These timing differences can act as efficient precopulatory isolation mechanisms (Reise 1995, Wiktor 2000). For example, individuals from allopatric populations of *Deroceras rodnae* Grossu and Lupu, 1965 and *Deroceras praecox* Wiktor, 1966 court with each other in the laboratory, but there is no overlap of the species-specific durations of courtship. The slug with the shorter courtship phase (*D. praecox*) proceeds to the copulation phase (*i.e.*, everts the penis) when its partner is still at early courtship. Because there is no receptive partner (*i.e.*, not another everted penis to entwine with), the *D. praecox* individual retracts its penis together with its own ejaculate, and mating is broken off (Reise 1995).

In most species in which mating has been observed, the courtship phase (or precopulatory phase) lasts much longer than the copulation and takes up most of the mating. The shortest known courtships, in *Deroceras reticulatum* and *D. praecox,* take about 15-20 min (but courtship can take longer in both species) and the longest courtship takes more than 7 h (*D. gorgonium*; the entire precopulatory phase may take 9 h: Reise *et al.* 2007).

The copulation is usually very brief compared to the

Table 2. Duration of different mating phases in *Deroceras*.

Species	Precourtship	Courtship	Copulation	Withdrawal	Reference
D. agreste		>48 min	30 s		H. Reise, unpubl. obs.
		>20->50 min	>60 s		Gerhardt 1933, 1934
D. gorgonium	95-276 min	145-434 min	18-25 s		Reise *et al.* 2007
D. laeve			up to 60 min		Barker 1999
Kazakh *D. laeve*		60-70 min (including precourtship?)	30-50 s	long (apophallation)	Rymzhanov 1994
D. lombricoides		up to >60 s	long		Simroth 1891
D. panormitanum			>10-15 min		Webb 1961
		>20-30 min	>10-15 min		Barker 1999
		up to >45 min	<3-12.5 min	usually 3-5 min	Gerhardt 1939
		ca. 50-80 min	ca. 3-12 min		H. Reise, unpubl. obs.
	0-28 min (mean = 12.5 min)	44-107 min (mean = 66.7 min)	0.8-9.5 min (mean = 2.7 min; without penial gland eversion)	0.7-5.1 min (mean = 2.6 min)	Benke 2006
D. planarioides		ca. 60 min	≤10 s until start of penis retraction		Gerhardt 1939
D. praecox		20-60 min	30-60 s		Reise 1995
D. rethimnonensis		ca. 30 min			Wiktor 1994
D. reticulatum		30->90 min	<15 s		Simroth 1885
		>45 min	28-49 s		Gerhardt 1933, 1934
		up to >70 min	ca. 30 s		Wiktor 1960
		30-almost 120 min	<60 s		Karlin and Bacon 1961
		15-36 min	"seconds, or at most a few minutes"		Webb 1961
		65 min	ca. 30 s		Nicholas 1984
		30-75 min	ca. 30 s		Barker 1999
D. rodnae		95-200 min	30-60 s		Reise 1995
D. sturanyi	usually >10 min	usually 30-40 min (up to 70 min)	"a few hours"	"some time"	Kosińska 1980
	15-120 min	52-169 min	60-144 min	1-70 min	H. Reise and C. Natusch, unpubl. obs.
			>19-71 min		Gerhardt 1936
		26-71 min	140-168 min		Rymzhanov 1994
D. turcicum		longer than *D. reticulatum*	very fast		Gerhardt 1935
		up to >240 min	ca. 20 s		H. Reise, unpubl. obs.
D. caucasicum	90-210 min*		3-4 min		Rymzhanov and Schileyko 1991

* refers to precourtship and courtship

precopulatory phase, and penis eversion starts rather suddenly, often almost explosively. At one extreme, copulation lasts only about 20 s in *Deroceras turcicum* (Simroth, 1894) (Gerhardt 1935, H. Reise, unpubl. obs.) and perhaps only 10 s in *Deroceras planarioides* (Simroth, 1910) (exact end of copulation unclear; Gerhardt 1939). However, copulation can last considerably longer and, at least in one species, can even take longer than the courtship (*D. sturanyi* has a 26-71 min courtship and a 60-168 min copulation: Kosińska 1980, Rymzhanov 1994, H. Reise and C. Natusch, pers. obs.).

The durations depend also on temperature (Wiktor 1960, 2000, Karlin and Bacon 1961, Kosińska 1980, Rymzhanov and Schileyko 1991) and possibly humidity and light regime (Rymzhanov and Schileyko 1991). There is also con-

siderable intraspecific variability (Table 2). Karlin and Bacon (1961) observed that even in couples of *Deroceras reticulatum* mating at the same time, the duration of precourtship varied by a factor of three.

PRECOURTSHIP PHASE

The initial mating behavior, lasting until eversion of both sarcobela, is the phase with the least published information about it, because casual observations are usually made when mating has already started. Probably in all species the partners initially investigate each other with their tentacles and mouth and eat the partner's body mucus (Kosińska 1980, Rymzhanov 1994, Reise 1995, Wiktor 2000).

Many species show some degree of trail following, which can constitute a major part of the precourtship phase. This behavior has been described as simple directional following of one slug along the mucus trail of another to catch up with a potential mating partner (Wareing 1986, Wiktor 2000) and has sometimes also been called a chase (Gerhardt 1933, Webb 1961). However, my own observations indicate that trail following during the recognition phase is a complex behavioral pattern involving the active participation of both partners. Usually the partner following keeps very close to the leader. In *Deroceras panormitanum* and other species with pronounced trail following, the tail is flattened laterally and becomes a flag-like structure (Fig. 5); it is slightly lifted up above the ground, and waves side-to-side, either in front of the follower's head or between its tentacles, thus contributing to the occasional contacts between tail and tentacles. If the follower falls behind, the leader seemingly tends to wait for it, tail waving. It would be interesting to conduct experiments in the dark to test whether tail waving acts as a visual stimulus, but it might also emit a chemical attractant.

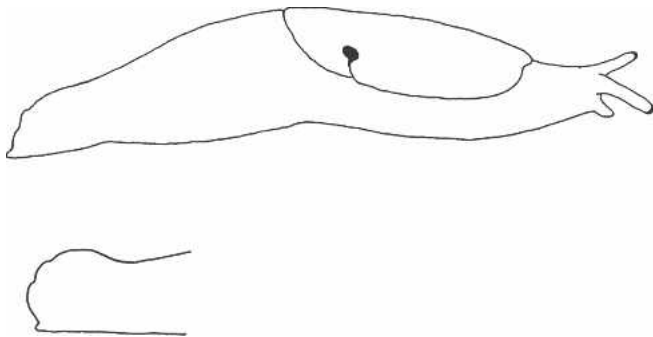Trail following has been observed in *Deroceras panor-*

Figure 5. Tail enlargement during trail following in *Deroceras panormitanum*.

mitanum (H. Reise, unpubl. obs., Benke 2006, but see below), *D. gorgonium* (although little pronounced, Reise *et al.* 2007) and *D. sturanyi* (Kosińska 1980, Rymzhanov 1994). It was described as a regular component of mating in *D. reticulatum* by Gerhardt (1933), Quick (1960), and Wareing (1986), but Webb (1961) and Barker (1999) indicated that it occured only occasionally. I observed that it did not occur in *D. rodnae* and *D. praecox* (Reise 1995, 1997); Barker (1999) stated that it did not occur in *D. laeve*; but Rymzhanov (1994) did describe it in Kazakh *D. laeve*. The fact that it was not mentioned by Gerhardt (1936, 1939) for *D. planarioides* and *D. sturanyi* nor by Nicholas (1984) for *D. reticulatum* is more difficult to interpret.

The idea that trail following serves for catching up with a potential mate implies that the follower is the more active, mating-initiating partner. However, the tail waving indicates that the leader's role can be much more interactive than has been assumed. Moreover, in *Deroceras panormitanum* almost always, and in *D. gorgonium* usually, it is the leader that extrudes its sarcobelum first (Benke 2006, Reise *et al.* 2007, H. Reise, unpubl. obs.). Moreover, later in courtship, at least in *D. gorgonium*, this trail-leading partner is also the first to exhibit each successive behavioral pattern. In Kazakh *D. laeve*, the leader is the first to touch the partner during courtship and to retract its penis after copulation (Rymzhanov 1994). Thus, if there is a partner with an initiating role, it is probably the leading slug. However, this might differ interspecifically, because the follower everts its sarcobelum first in *D. caucasicum* (Rymzhanov and Schileyko 1991) and *D. sturanyi* (Rymzhanov 1994).

By the end of precourtship, the partners form an open circle with their heads towards the partner's tail and genital pores pointing towards the inside of the circle, and they often begin circling. In trail-following couples, this position is reached by the leading slug finally crawling in a bow back towards the follower, usually towards the latter's tail. This is often when the second partner or both partners evert the sarcobelum and start courtship.

The behavior and duration of the precourtship phase vary considerably, not only between species (Table 2) but also within species, probably owing to variation in the motivation to mate (Benke 2006, Reise *et al.* 2007, H. Reise, unpubl. obs.). Slugs in which isolation is likely to have generated a high motivation to mate tend to abridge the precourtship phase and may even move on to courtship soon after first contact (see below). This supports the suppositions that precourtship serves to assess a partner's readiness to mate (Wiktor 2000) and that some behavioral patterns might also aim at motivating a partner that does not show initial interest. A role in species recognition is also possible (Wiktor 2000).

Intraspecific variability might be the reason for some

discrepancies in descriptions of precourtship by different authors. For instance, trail following usually occurs in *Deroceras sturanyi* but can be skipped by some couples (Rymzhanov 1994). Probably more often, however, these differences may be caused by incomplete observations or differing opinions about whether a behavior should be considered part of mating. In *D. panormitanum*, for example, Webb (1961, 1965) and Barker (1999), based on observations of unspecified numbers of couples from France and New Zealand, reported that mating starts with circling (which occurs after trail following) and Gerhardt (1939, based on about 30 couples from Wales) even expressly stressed that there was no trail following. However, in the more than 150 matings of *D. panormitanum* from the UK, Belgium, the Netherlands, and Germany that I and my co-workers have watched, this behavioral pattern was almost always present, although occasionally very brief.

COURTSHIP PHASE

Courtship begins when both partners protrude their sarcobela; this is usually a rapid process. Eversion happens simultaneously (Wiktor 2000) or one soon after the other (Wiktor 2000, H. Reise, unpubl. obs.). In *D. panormitanum* this is a rather fixed process: as described above, the slug leading the trail following turns back towards the follower, and they then form a circle. Most often, the first slug everts at the moment of turning back, and the second slug everts soon after formation of the circle. However, sometimes the second sarcobelum has everted shortly before the circle is formed, or sometimes the first sarcobelum everts shortly after circle formation (Benke 2006, H. Reise, unpubl. obs.). In contrast, sarcobelum eversion in *D. gorgonium* is quite variable: often one slug everts long before the other and may retract repeatedly. However, eversion can also be almost simultaneous in this species, and the temporary retractions do not always occur. This causes a highly variable duration of the precourtship (95-276 min) and courtship phases (145-434 min) in this species. However, the duration of the entire precopulatory phase varies much less than each component phase (about 7-9 h); so a long precourtship is followed by a short courtship and *vice versa* (Reise *et al.* 2007).

Kosińska (1980) reported that the sarcobela are "generally, although not always" everted during courtship of *Deroceras sturanyi*. It is unclear whether she meant that one or both partners might not evert the sarcobelum at all during courtship (which would be unique amongst *Deroceras*), or whether it had already been everted earlier.

Stroking the partner with the sarcobelum, or at least apparent efforts to use it to touch the partner, are the most prominent aspects of courtship. As soon as the sarcobela are everted, the slugs direct them towards their partners, and by then they have formed a configuration with their genital pores facing towards one another; often this is a circular configuration. Sooner or later, the partners position themselves more and more into a yin-yang position: each head is at the partner's side and the genital openings thus lie close to each other (Fig. 4B-C). A tight yin-yang is the position for copulation. In all species, slugs get progressively closer during courtship and stroking intensity progressively increases but stops just before copulation.

There are large interspecific differences in the duration of the courtship phase (see section on timing), the intensity and speed of circling, the position of the partners towards each other, the way of stroking, and to what extent there is an aggressive component. I now discuss these in turn.

All species show some circling during most of the courtship (Barker [1999] stated that there is no circling in *Deroceras laeve*, but see the introduction section about my doubts). Circling is almost always clockwise and more or less around a central point which hardly moves. If each partner follows the other's tail, they form a circle; if each crawls towards the other's right side, they assume the yin-yang position; in both cases I term the movement "circling". Occasionally, one partner may leave the position and circle one or two turns around its own axis or around a slower partner, but it will always return into the original circle or yin-yang configuration (Wiktor 1960, Rymzhanov and Schileyko 1991, H. Reise, unpubl. obs.).

Most species start with a circle and then slowly change towards yin-yang, as in *Deroceras reticulatum* (Gerhardt 1933, Webb 1961, H. Reise, unpubl. obs.), *D. sturanyi* (Kosińska 1980), and *D. caucasicum* (Rymzhanov and Schileyko 1991). Others are in the yin-yang position from a very early stage (*D. rodnae*, *D. praecox*, *Deroceras fatrense* Mácha, 1981: Reise [1995, 1997, unpubl. obs.]). *Deroceras gorgonium* seems unusual in that almost the entire courtship consists of two alternating behavioral patterns: individuals wave their sarcobela whilst remaining stationary (see below) and then circle half a revolution (so that each slug ends up in its partner's former position).

The speed of circling generally decreases later in courtship. Kosińska (1980) distinguished two phases of courtship in *Deroceras sturanyi*: (i) a "quick circular dance" in a larger circle, with the mouth and sarcobelum touching the partner's tail, lasting usually for 20-30 min, but sometimes more than 1 h and (ii) a "slow circular dance" in a smaller circle, lasting about 10 min and occasionally interrupted by 40-65 s bouts in the yin-yang position when their sarcobela and mouths touch the area around the other's genital opening. During the "quick dance", the partners needed usually 20-60 sec to complete one circle, and during the "slow dance", 60-90 s. The decrease of circling speed in *D. sturanyi* was also

noted by Gerhardt (1939) and Rymzhanov (1994), although Rymzhanov's timings are contradictory: first 80-95 s per revolution, and later 68-75 s. Specimens of Kazakh *D. laeve* take 1.5-2.5 min during early courtship and 4.5-5 min later (Rymzhanov 1994). Also in *D. caucasicum*, circling is faster at the beginning (2 min per circle) than later (10-12 min) (Rymzhanov and Schileyko 1991).

All sarcobela, particularly the larger ones, are very maneuverable organs and seem adapted for touching the partner and for transferring a secretion onto its body. It would make adaptive sense also if they had a chemosensory function in assessing the physiological state of the partner, but there is no evidence for this. As there is an enormous diversity of sarcobelum shapes and sizes (Fig. 3), it is not surprising that also their use varies considerably. Species with large, flat, tongue-like sarcobela appear particularly efficient at transferring secretions. Such sarcobela are usually laid flat onto the partner and stroked along its body. The large area of such sarcobela and their extremely flexible movements ensure that much body surface is covered. *Deroceras fatrense* and *D. rodnae* stroke mainly the partner's back and side, most often around the mantle, using the underside of the sarcobelum (although some individuals of *D. rodnae* also often use the narrow edge). *Deroceras praecox* strokes mainly the partner's lower flank and the sole using the upper side of the sarcobelum (Reise 1995, 1997, unpubl. obs.). There are many other species that have a flat sarcobelum, but their mating behavior has not been observed. So, it remains to be examined whether large flat sarcobela consistently stroke more intensely and closely than others (but see descriptions of *D. caucasicum* and *Deroceras lombricoides* (Morelet, 1845) below).

The majority of species have conical sarcobela, varying from rather short, stout organs to long, pointed, finger-like ones. The medium-long sarcobela of *Deroceras reticulatum*, *D. agreste*, *Deroceras nitidum* (Morelet, 1845), and *D. sturanyi* are used to stroke the partners during almost the entire courtship, but the limited length and maneuverability permit touching only the facing flank of the partner, and the conical shape does not allow very broad contact. The rather aggressive *D. panormitanum* touches considerably less frequently and less intensely during the first part of courtship than other species with similar sarcobela (see below).

Short bump-like sarcobela such as in some *Deroceras laeve* (Wiktor 2000) surely cannot stroke as well as longer ones and must reach the partner only when it is very close. This is one reason why I suspect that published descriptions of *D. laeve* mating behavior (Gerhardt 1936, Karlin and Bacon 1961) have dealt with different species (see also the introduction section). In Kazakh *D. laeve*, Rymzhanov (1994) seems to have seen more touching with the mouth than with the sarcobelum. Detailed descriptions of the

courtship of species with such rudimentary sarcobela would be highly valuable.

At the other extreme, *Deroceras gorgonium* has a very long, slim sarcobelum with a sharply pointed tip. There is almost no body contact during early courtship (which can last for several hours), and the sarcobelum, stretched out perpendicular to the body, merely waves in front of the partner's face. Only later do the partners get closer, but even then for much of the time the sarcobela touch each other or the partner's body just with their tips. We have occasionally observed transfer of secretion droplets via the tip of the sarcobelum (Reise *et al.* 2007). Maybe the sarcobela are so long in this species to bridge the long distance between partners and to apply the secretion, and animals might keep so far apart to avoid receiving the secretion. Secretion droplets have also been observed on the sarcobela of courting *D. caucasicum* (S. Leonov, pers. comm.).

There are a few species for which the stroking behavior is unusual in some way, and reexamination would be desirable. Rymzhanov and Schileyko (1991) describe the mating of *Deroceras* (*Liolytopelte*) *caucasicum* from some introduced Kazakh populations (Wiktor 2000) where the sarcobelum is used for intense stroking but, judging from their published figures, the partners seem to take up the yin-yang position only shortly before copulation. Their figures show a large flat sarcobelum covering rather large parts of the partner's body. However, there are contradictory opinions about whether the sarcobelum is like this (Rymzhanov and Schileyko 1991, Likharev and Wiktor 1980) or conical (Wiktor 2000, S. Leonov, personal communication: photographs of mating couples from the Crimea). This might reflect geographical differences between populations or indicate different taxa.

The sarcobelum of *Deroceras lombricoides* is also flat, but unusually thin, wide and very short (Wiktor 2000). At eversion, it resembles the arionid ligula (Wiktor 2000), and one wonders how this fold-like structure can stroke a partner. However, a huge flat lobe is pressed onto the partner's back during courtship (fig. XI in Simroth 1891, Castillejo *et al.* 1989), so it seems that the bulky, distal part of the penis is everted through the genital pore together with the horseshoe-like fold mounted upon it.

The courtship of *Deroceras* (*Liolytopelte*) *bureschi* (Wagner, 1934) also appears to be unusual, although the scanty description is based on only a single field observation (Wiktor 1983, personal communication). The "inconspicuous" sarcobelum (Wiktor 2000) is so small that it is not even mentioned in an earlier anatomical description (Wiktor 1983) and hardly recognizable on the genital drawings (Wiktor 1983, 2000). During courtship, it is protruded together with an everted finger-like penial appendix assumed to be homologous to the penial gland (Wiktor 2000), and the partners are described as stroking each other with this struc-

ture rather than with the sarcobelum (Wiktor 2000, fig. 36). This would be the only known case in *Deroceras* where a penial appending structure is already everted during courtship and used for stroking. The calcareous plate of *Liolytopelte* seems not to be used during courtship except that partners of *D. caucasicum* lick the mucus off it, perhaps to prepare it for sperm exchange (Rymzhanov and Schileyko 1991; see copulation section). However, this behavior was not mentioned for *D. bureschi*, the only other species of *Liolytopelte* whose mating behavior has been observed (Wiktor 1983, 2000).

The sarcobelum of *Deroceras turcicum* is very polymorphic, varying from conical to a flat tongue, and from short to rather long (Reise and Hutchinson 2001a). The observations of mating (Gerhardt 1935, H. Reise, unpubl. obs.) indicate much similarity to *D. reticulatum*. However, it would be interesting to test whether stroking intensity and efficiency vary intraspecifically with the shape and size of this organ.

Slugs also differ in how close they get during courtship and whether there is an aggressive component in the behavior. While some species (particularly the ones with a large, flat sarcobelum) are very close from the beginning and show no, or hardly any, aggression (*e.g.*, *Deroceras rodnae* and *D. praecox*), other species keep very distant (*e.g.*, *D. gorgonium*, see above), and some regularly exchange biting attacks during the early courtship phase. Occasional biting has been observed in *D. reticulatum* (Webb 1961; Karlin and Bacon [1961] mentioned "pugnacious" strikes with the head, probably for slime feeding), *D. agreste* (Gerhardt 1933), and *D. gorgonium* (Reise *et al.* 2007).

In the particularly aggressive species *Deroceras panormitanum*, the aggression prevents them from getting close until the later stages of courtship. In this species partners initially exchange vigorous bites whenever they get closer or one tries to touch the other with its sarcobelum. Strikes onto the flank, tail, sarcobelum or head are often recognizable as bites rather than mere "licking", and the partner usually reacts with a short backward movement, frequently followed by an attack in response. The movements of the stretched sarcobela look like fencing matches in which the partners try to stroke but not to be stroked. However, bites and strokes often do not hit the partner, and many bouts of such aggression look like ritualized duels. As they do during trail following in this species, the tails seem to play an important role in the early phase of courtship: slightly lifted up from the ground and still enlarged, they are often waved just in front of the partner's face, possibly distracting the partner's biting attacks from more sensitive genital and head regions. There is strong tail lashing during phases of mutual attacks and particularly when being bitten. However, after a while, the partners slowly become less aggressive, their separation

decreases, and the sarcobela finally stroke as intensely as in other species such as *D. reticulatum* (H. Reise, unpubl. obs.). *Deroceras planarioides* also exhibits much aggression and tail lashing (Gerhardt 1939).

Just before the start of copulation, the sarcobela are slightly contracted and point more or less upwards (Simroth 1885, Gerhardt 1933, Wiktor 1960). The genital openings and the bases of the sarcobela are pressed against those of the partner (Gerhardt 1933, 1936, 1939, Nicholas 1984, Rymzhanov 1994, Reise *et al.* 2007). Mouth and tentacles may "fumble" around the genital pore (*e.g.*, Gerhardt 1939, Webb 1961, H. Reise, unpubl. obs.). The anterior parts of the bodies swell, lie slightly over onto their left, and the mantles are pulled backwards. Although circling stops, the partners may entwine the anterior parts of their bodies in an even tighter position just before penis eversion. Usually, particularly when one partner shows some apparent reluctance, the slugs take up this position repeatedly, but the "reluctant" partner will always loosen the contact again before mutual penis eversion finally begins (Nicholas 1984, Reise *et al.* 2007). This is probably what Castillejo *et al.* (1989) observed in *Deroceras nitidum* and interpreted as two different, alternating kinds of stimulation: sarcobela opposite one another (the figures imply that tentacle and sarcobelum touch areas near the genital pore) alternating with stroking the partner's flank.

Kosińska (1980) reports a short transitional stage in *Deroceras sturanyi*: the sarcobelum and the "remaining parts of the copulatory organs" are everted and retracted before copulation starts. There must be some intraspecific variability, because we observed this only in one out of six matings (H. Reise and C. Natusch, unpubl. obs.). Short, partial penis eversion preceding copulation was also observed in *D. reticulatum* (Nicholas 1984).

During courtship, the ejaculate is assembled within the penis. In *Deroceras reticulatum*, sperm starts flowing from its storage site (the ductus hermaphroditicus) 10 minutes after the start of courtship, and it first appears in the penis after 20 minutes. Ten minutes later, all sperm has arrived in the penis, and within a further 10 minutes the prostate secretion has completed the sperm package (Nicholas 1984). In *D. panormitanum*, sperm was not found in the penis 10 minutes after the start of courtship, but there was an ejaculate in a specimen killed after 30 minutes (Benke 2006). Nothing is known about other species. However, it would be particularly interesting to compare these data with those from species with very short or very long courtships.

COPULATION

Copulation is the phase of sperm exchange and lasts from the start of penis eversion to the moment when the

genitalia lose contact with the partner. The two everted penes swell to several times their normal size (Nicholas 1984). They appear as a bulbous, bluish transparent mass lying between the partners, and it is hard to distinguish component parts.

The speed of penis eversion and the overall duration of copulation vary considerably. Most common is a sudden, sometimes explosive, eversion and a very short copulation compared to the duration of courtship. Some species, such as *Deroceras gorgonium* and *D. turcicum*, reach maximum eversion within one second (Reise *et al.* 2007, H. Reise, unpubl. obs.). The high speed requires video-recording to discriminate the sequence of events (although video may sometimes not suffice because of the difficulty in distinguishing the parts of the penis; rapid killing of couples at different stages of copulation is thus also helpful). For this reason, most published descriptions give only an overall duration of copulation, and it is often not clear whether this includes a part of or the entire withdrawal.

As they evert, the penes entwine, in some species more tightly than in others, and they press against each other in an apparently species-specific way. The entwinement is achieved by a sickle-like curve of the everted penial bags. The shape of the penis must matter considerably for a successful "embrace" and sperm exchange. The proximal ends of some penes may even be spiral (*e.g.*, Figs. 2K-L), which might facilitate close entwinement. The extreme is *Deroceras helicoidale* Rähle, 1998 with its spectacularly prolonged, helically coiled, penial bag (fig. 2G, Wiktor 2000), but nothing is known of its copulation. In this and many other species, the curve of the penis is evident even when retracted, but in other species the curve is generated only on eversion as a result of the insertion site of the penial retractor muscle (Simroth 1885, Gerhardt 1939, Wiktor 1960). Rymzhanov (1994) stresses that Kazakh *D. laeve* differs from other *Deroceras* in that the penes are pressed less intensely against each other; he does not mention any entwinement.

There is no spermatophore, and the ejaculate is transfered as an amorphous soft mass. Simroth (1885) described the ejaculate found in the penis of *Deroceras reticulatum* before sperm exchange as fine strings rolled up into roundish bodies and surrounded by a mucous layer. At least in this species, the sperm are indeed packed in several discrete bundles and wrapped by several layers of secretions produced by the prostate (Nicholas 1984; her thesis also details secretion activities of other parts of the genital tract at successive mating stages). Simroth's assumption (1885) that the sperm mass of *Deroceras* is a precursor of spermatophores is incompatible with current knowledge of the phylogeny (Hausdorf 1998). Rather, it is probably an adaptation to a copulatory system with external sperm exchange (Nicholas 1984).

At copulation, the ejaculate is everted together with the donor's penis and transferred onto the surface of the receiver's everted penis; both partners donate and receive simultaneously. The retraction of the penis then takes the ejaculate with it (Webb 1961, 1965, Nicholas 1984, Reise 1995, unpubl. obs., Wiktor 2000, Benke 2006). In the few species for which details of sperm exchange are known, it happens at the peak of penis eversion and thus very early in copulation; this is irrespective of how long the entire copulation lasts (Reise 1995, 1997 [*Deroceras praecox*, *D. rodnae*, *D. fatrense*], Benke 2006 [*D. panormitanum*], Reise *et al.* 2007 [*D. gorgonium*]). Even in *D. sturanyi*, a species with an extremely long copulation phase, sperm exchange happens early in copulation, although the transfer is slightly slower in this species (Gerhardt 1936). It remains to be investigated what happens during the rest of the copulation in such species with long copulations. Spasms on the body surface of *D. sturanyi* (Kosińska 1980) indicate activities of internal organs. In other taxa, copulations continuing after sperm exchange have been supposed to represent efforts of donors to prevent sperm digestion and thus help the sperm reach the sperm storage site (Michiels 1998).

The ejaculate seems to be transferred from a particular area of the donor's penial wall onto a particular area of the recipient's penial wall. In *Deroceras gorgonium*, the ejaculate is "slapped" onto the partner's penis (onto an area on the wall just distal to the base of the sarcobelum), and the donating part of the penis slackens immediately after this. In *D. reticulatum*, the ejaculate is collected at the base of the penial gland in the donor's penis and transferred onto the folds in the proximal part of the receiver's penis (Webb 1961, Nicholas 1984).

The majority of *Deroceras* species have one or more glandular penial side pockets (Sirgel 1973, Wiktor 2000). At least in *D. praecox*, *D. panormitanum*, and *D. gorgonium* these are everted during copulation (Webb 1961, 1965, Benke 2006, Reise *et al.* 2007, H. Reise, unpubl. obs.). Their functions are largely unknown, but, at least in some species, one pocket seems to serve as an ejaculate-holding bag prior to transfer, probably to ensure a more exact positioning of the ejaculate onto the partner's penis. The function of the additional bags occuring in a number of species is unknown. Most is known about *D. panormitanum*. The penis of this species has two side pockets: the longer one ("terminal lobe" of Webb 1961, 1965, "longer penial diverticle" of Sirgel 1973) is everted at the beginning of copulation and slackens immediately after maximum eversion; the shorter one ("medial lobe" of Webb 1961, 1965, "shorter penial diverticle" of Sirgel 1973) is everted slightly later (Benke 2006), or considerably later (Webb 1961), pressed onto the partner's shorter pocket and remains inflated for a longer time, during which pumping movements of the penial mass can be ob-

served (Benke 2006). The longer pocket is filled with the sperm mass during courtship (Sirgel 1973, Benke 2006) and it also adds its own, probably holocrine, secretions (Sirgel 1973). At eversion, the curved longer pocket is laid around the base of the receiver's sarcobelum, to which the ejaculate is then attached (Benke 2006). Little or no sperm can be found in the shorter side pocket (Sirgel 1973, Benke 2006). This has a different internal structure from the longer pocket and produces two different types of secretions (Sirgel 1973). Sirgel (1973) assumes that these secretions are added to the ejaculate during the eversion process, but while it is still in the lumen of the penis. In that case, it is be puzzling why this shorter pocket is everted later than the other one and remains inflated for so long. However, this secretion must be the reason why Webb (1961) thought that the ejaculate is transferred with the second, shorter pocket. The latter was also reported by Barker (1999) but the perfect agreement between these publications suggests that Barker based his account on Webb's.

During courtship of *Deroceras caucasicum*, the sperm mass is put into, and wrapped by, an albumen membrane extended like a hammock within the donor's penis between two nodular appendices. This package is then laid onto the receiver's calcareous plate during copulation (Rymzhanov and Schileyko 1991). This is apparently the function of the plate, whose presence defines the subgenus *Liolytopelte*.

In *Deroceras panormitanum*, *D. caucasicum*, *D. reticulatum*, *D. sturanyi*, and Kazakh *D. laeve*, the ejaculate is transported through the vas deferens into the penis before copulation starts (Simroth 1885, Wiktor 1960, Webb 1961, Nicholas 1984, Rymzhanov and Schileyko 1991, Rymzhanov 1994, Benke 2006). However, Gerhardt (1933) and Reise (1995) reported seeing the ejaculate being expelled through the vas deferens during copulation of *D. agreste* and *D. rodnae* respectively. Gerhardt (1939) reported this also for *D. panormitanum*, which is in conflict with other, more thorough, studies of this species based on rapid killing at different mating stages (Webb 1961, 1965, Benke 2006). This calls for a critical reexamination in *D. agreste* and *D. rodnae* using the rapid-killing technique.

The ejaculate is visible either during the entire process of sperm exchange or at least when the slugs separate. In at least some species, the ejaculate forms a longish package, sometimes stretched so much that one end still sticks out of the genital orifice when the penis is fully retracted. The color of ejaculates varies between white and yellow (Gerhardt 1933, 1936, 1939, Wiktor 1960, H. Reise, unpubl. obs.); it is white in *Deroceras praecox* but yellow in its sibling species *D. rodnae* (Reise 1995).

Species that have an appending penial gland (at the proximal end of the penis, Fig. 1) evert it during copulation (Simroth 1885, Gerhardt 1933, 1939, Webb 1961, 1965, Ni-

cholas 1984, Castillejo *et al.* 1989, Reise 1995, Wiktor 2000, Reise *et al.* 2007. Runham (1978) wrongly wrote that it is everted during courtship in *Deroceras reticulatum*, and Wiktor (1983, 2000) suggested this for *D. bureschi*—see section on courtship). In species in which the gland is sufficiently large, it usually spreads over the partner's body (Fig. 6; Webb 1961, 1965, Nicholas 1984, Castillejo *et al.* 1989, Reise and Hutchinson 2001b, Benke *et al.* 2005, Benke 2006, H. Reise, unpubl. obs.). This eversion is striking in species with a large gland (*e.g.*, *D. panormitanum*), which can span most of the body length. The gland is always everted for only a short time and retraction starts immediately after full eversion (Webb 1961, Reise 1995, unpubl. obs., Benke 2006). However, the timing varies between species. In some species with a very sudden and quick copulation, the partners evert their glands more or less simultaneously along with the full penis eversion and sperm exchange (Reise 1995, unpubl. obs.). However, in *D. gorgonium*, where copulation is also very quick, video recording showed that the highly branched glands are everted immediately after the ejaculate has been transferred onto the receiver's penis (Reise *et al.* 2007). Similarly, Wiktor (1960) and Webb (1961) observed that in *D. reticulatum* the gland is everted at the end of copulation when other parts of the penis are collapsing. In *D. panormitanum*, the comparatively slow copulation makes it even clearer that gland eversion is after sperm exchange, when the other parts of the penis have begun to retract (Fig. 5; Webb 1961, Reise and Hutchinson 2001b, Benke *et al.* 2005, Benke 2006). Moreover, the second partner begins to evert its gland only when the first partner has finished, or almost finished, retracting its penis and gland and often has already started to crawl away. Particularly in the latter case, some or all fingers of the gland may miss their target and spread on the ground (H. Reise, unpubl. obs.). Benke (2006) observed intervals of 10-72 s (mean = 32 s) between the eversions of each partner's gland, but she did not find a clear difference in the
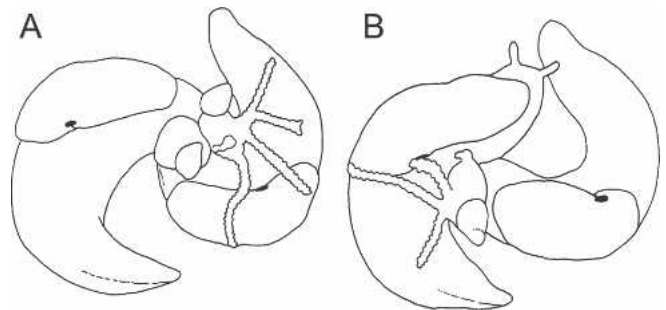

Figure 6. Eversion of the penial gland in *Deroceras panormitanum*. A, Maximum eversion of the left slug's gland. B, Eversion of the right slug's gland; the partner has already retracted and is crawling away. Drawn from two video frames.

success of first and second gland eversions: out of 35 matings, Benke observed full or partial misses for the first eversion in four cases and for the second in three cases.

The only report that the penial gland of one partner does not evert during a copulation is from two matings (out of 27) of *Deroceras panormitanum* (Benke 2006, personal communication). The penial gland of one of these slugs was still filled 120 min after copulation, indicating that the secretion had been produced but not transfered. The penial gland of the other slug, killed after 30 min, was empty; it might not have produced a secretion or eversion might have been overlooked. It can be difficult to spot the eversion if the gland spreads underneath the partner's body, as appears to be common in *D. gorgonium* (Reise *et al.* 2007). Nothing is known about how species with a very small penial gland, such as *D. agreste,* use it.

The function of the penial gland is not known. Webb (1961) assumed that it functions for "semen-securing and retaining" during retraction, but there is no evidence for this (Nicholas 1984, Benke 2006, H. Reise, unpubl. obs.). However, the observation that it is everted only after sperm exchange in *Deroceras panormitanum* has prompted the hypothesis that it transfers a secretion to manipulate the partner physiologically so as to increase the chance of paternity (Reise and Hutchinson 2001b; *cf.* the proven function of the dart in *Cornu aspersum* [Müller, 1774]; Koene and Chase 1998, Rogers and Chase 2001, 2002, Landolfa *et al.* 2001, see also the discussion section). The secretion would thus act as an allohormone (Koene and Ter Maat 2001). Histological studies and direct observations have shown that the penial gland is filled up during early courtship and that this secretion is transferred onto the partner's skin (Nicholas 1984, Benke et al. 2005, Benke 2006). Observations that mating partners in *D. panormitanum* try to lick off this secretion from their own body just after copulation (Benke 2006) might be efforts to escape manipulation by the partner. At least some of the secretion accumulating in the penial gland before copulation is transferred from the prostate (Nicholas 1984), but there are also indications of aprocrine secretion in the penial gland itself (Sirgel 1973, Nicholas 1984, Benke 2006).

Although the usual mode in *Deroceras* is simultaneous mutual sperm exchange, unilateral sperm transfer occurs occasionally. In *D. rodnae*, Reise (1995) observed a few such cases associated with unusual behavior of the sperm donor. The donor slug tried to keep contact with the recipient by following, with genitalia still partly everted, but the recipient fully retracted its genitalia and showed no further interest. I. Schulze (pers. comm.) did not find an ejaculate in 6 out of 105 individuals of *D. panormitanum* killed immediately after copulation. Benke (2006) killed couples of the same species 10–90 min after copulation and found that in 9 out of 39

individuals there was no ejaculate in the penial sac (where the received sperm mass should have been). At least 4 of the partners of these 9 slugs had one sperm package in their penial sac as well as another one in the long side pocket; that is, one ejaculate that they had just received and one prepared for donation. Gerhardt (1933) reported ejaculates of *D. reticulatum* which missed the receiver and ended up on the ground (I. Schulze [pers. comm.] observed another instance). Such lost ejaculates, or partial ejaculates, are also implied by Nicholas' (1984) statement that after copulation *D. reticulatum* eat remaining sperm along with accumulated mucus. Cases of unilateral sperm exchange where an ejaculate was produced but not donated successfully (either kept by the sperm owner or lost during transfer) might represent accidents. Alternatitively, they might be caused by one partner deliberately not performing one of the two sexual roles. Cheating on the reciprocal sperm exchange by avoiding donating sperm is an unlikely explanation, because this partner has paid much of the cost of the male role by having produced an ejaculate. However, deliberate sperm rejection by a receiver would be more plausible. Sperm rejection (or eating) might be advantageous over sperm digestion in the bursa copulatrix if the ejaculate contains manipulating substances causing costs to the receiver.

Kosińska (1980) observed several couples of *Deroceras sturanyi* in which only one partner fully everted the penis, and she concluded that only one partner received sperm. However, I doubt that any sperm transfer took place because this must surely require not only a donating but also a receiving penis. This is also relevant to the question of whether aphallic indviduals of *D. laeve* can receive sperm from an euphallic individual (see sections on genital morphology and withdrawal). The only other recorded cases of unilateral penis eversion are from mixed couples of two different species, *D. praecox* and *D. rodnae* (Reise 1995; see section on timing).

Webb (1961) noted that copulating *Deroceras reticulatum* "invariably" take up their own ejaculate or a mixture of both partners' ejaculates, but he did not indicate what evidence prompted this conclusion.

The duration of the copulation phase varies remarkably between species (Table 2). Gerhardt (1939) classified *Deroceras* into two groups: (1) species with short copulations during which partners entwine further: *D. reticulatum*, *D. agreste*, *D. turcicum*, and *D. planarioides*; (2) species with long copulations during which partners do not entwine further: *D. panormitanum*, *D. lombricoides*, and *D. sturanyi* (which he called *D. laeve*, see introduction; mistakenly, on p. 199, he listed *D. reticulatum* and *D. agreste* instead). *Deroceras fatrense*, *D. gorgonium*, *D. praecox*, *D. rodnae*, and Kazakh *D. laeve* should now be added to the fast group. Gerhardt's (1939) hypothesis of a consistent association between speed of copulation and further entwining during copula-

tion must now be rejected: *D. praecox*, a species with a very fast copulation, does not entwine further. Instead, the partners are even pushed apart by the everting penial mass (H. Reise, unpubl. obs.). I observed the same phenomenon in video-recorded copulations of *D. turcicum* (H. Reise, unpubl. obs.), which is in disagreement with Gerhardt (1935). However, he might have worked with a different species (he called his slugs "*D.* aff. *turcicum*").

The species with "fast" copulations form a rather homogeneous group with a copulation time of less than one minute. In contrast, the "long" copulations of the remaining species vary from three minutes to several hours and their intraspecific variability is much higher: about 3-12 min in *D. panormitanum* and 60-148 min in *D. sturanyi* (Table 2). Examination of additional species may well establish more of a continuum between the groups with short and long copulations, but even then the variation in duration would remain to be explained.

WITHDRAWAL

Irrespective of whether the copulation is short or long, penis retraction is usually a rather fast and straightforward process once started (Gerhardt 1935, 1936, 1939, Reise 1995, unpubl. obs.) although it is much slower than the eversion. There are a few exceptions: (i) delayed or only partial retraction by one of the partners in rare cases of unilateral sperm exchange (see preceding section); (ii) late eversion of the penial gland in *Deroceras panormitanum* when the main part of the penis is already retracting (see preceding section); (iii) one partner remaining inactive at the mating site with fully everted penis in *D. sturanyi* (sometimes) and Kazakh *D. laeve* (always), with or without apophallation (see below). Because eversion of the penial gland probably plays an important role and overlaps other components of copulation, I include gland eversion as part of the copulation phase and define the end of the copulation phase (and the start of the withdrawal phase) as when the genitalia no longer have any contact with the mating partner. As a consequence, penis withdrawal and sperm uptake may start before the withdrawal phase.

The most common mode seems to be that both partners withdraw more or less simultaneously, performing intense pumping and rocking movements with the anterior body. As soon as the genitals untangle, the slugs separate and may crawl away from each other before finishing withdrawal. Usually the partners show no further interest in each other, with the exceptions (i) and (iii) mentioned in the preceding paragraph. The sarcobelum is the last part to disappear inside. Some ejaculate may stick to the last genital parts to remain everted, and then the slug may turn its head to its

genital orifice and apparently push the sperm mass in (Reise 1995). However, Benke (2006) observed two cases in *Deroceras panormitanum* where one partner tried to eat ejaculate sticking to its own, not yet fully retracted, genitalia. So the question of whether the slugs are assisting uptake of the ejaculate or eating it (*cf.* Karlsson and Haase 2002) needs reinvestigation. Eating could also be a last resort if the uptake is going to fail, similar to when the ejaculate has been lost onto the ground.

Some unusual behaviors during the withdrawal phases have been reported in *Deroceras sturanyi* and Kazakh *D. laeve*. Probably in many matings of *D. sturanyi*, only one partner retracts its penis immediately after copulation and crawls away. The other partner remains motionless at the mating site for some time with its penis still everted and slowly retracts it later. Kosińska (1980) apparently observed this in all matings but unfortunately does not tell how many she observed or how much later the second partner retracted. We found a very high variability in the mating behavior of *D. sturanyi* collected in Germany, only about 200 km away from Kosińska's population. In only one out of six full matings did one partner retract its penis considerably later (70 min) than the other. In four cases, both partners retracted more or less simultaneously, with not more than one minute difference. In one pair, one partner left only the sarcobelum everted, which was retracted after 25 min (H. Reise and C. Natusch unpubl. obs.). Rymzhanov (1994) and Gerhardt (1936) did not observe delayed retraction in any of the matings of 18 *D. sturanyi* from Kazakhstan or three matings of *D. sturanyi* from Germany.

Rymzhanov (1994) has reported retraction by only one partner as a regular pattern in matings of 12 Kazach *Deroceras laeve*. Moreover, the penis of the slug remaining at the mating site was not retracted later but bitten off by its owner and finally eaten by the other slug, which returned to the mating site and assisted amputation by pulling. Apophallation had previously been reported only from *Ariolimax* (Mörch, 1860), in which the penis may also be eaten by the partner (Leonard *et al.* 2002). These slugs are from a different family, Arionidae. They copulate by mutual or unilateral penis intromission and one penis (or both) is occasionally bitten off, usually after a period of struggle and pulling by the owner (implying that the penis gets trapped in the partner's genital tract (Mead 1943, Harper 1988, Heath in Pilsbry 1948: 710-711). Rymzhanov's (1994) observation of Kazach *D. laeve* is even more remarkable because the penis is not trapped in the partner's genital tract, and because apophallation is the rule rather than the exception. It seems hard to imagine a reason why an individual should voluntarily initiate amputation of its own penis; if it were the metabolic cost of keeping the organ when it will not be used again, it is puzzling why the slug does not eat it itself. One possible

explanation might be that the amputee has been manipulated by the partner by transfer of a secretion which inhibits retraction ability. The partner might be interested not only in gaining an additional food source but also in restraining it from remating and thus preventing sperm competition and/or shifting sex allocation towards the female function (the external mode of sperm exchange in *Deroceras* makes it improbable that individuals without a penis can donate or even receive sperm, in contrast with *Ariolimax* where aphallate individuals can still receive sperm because there is intromission [Leonard *et al.* 2002]). However, this explanation would only be plausible if the amputee has been able to take up the received ejaculate without penis retraction. Rymzhanov (1994) reported that the amputee was always the follower during precourtship trail following, so its fate was fixed at the start of mating. His paper further suggests that this apophallation is the origin of aphallic and hemiphallic individuals in *D. laeve* (see section on genital morphology). However, in German and North American populations of *D. laeve*, individuals that have grown up in isolation are often aphallic (Barth 2001, V. Barth and H. Reise, unpubl. obs., Reise and Hutchinson 2002, Jordaens *et al.* 2006). The phenomenon and the species identity are worthy of further investigation.

After full withdrawal, there is usually some eating of mucus by one or both partners. They may return to the mating site and lick the mucus-covered ground (Kosińska 1980, Nicholas 1984, Rymzhanov 1994, H. Reise, unpubl. obs.) or lick their own body surface (Benke 2006, H. Reise, unpubl. obs.), but there is much intraspecific variation. The function of this behavior is unknown. The mucus might simply serve as a nutritious substance. But a slug licking its own body might be trying to consume, and thus inactivate, an allohormone transferred by the partner by its sarcobelum during courtship or by its penial gland during copulation (see those sections).

Full withdrawal of all genital parts into their original position takes much longer than the withdrawal phase. The retraction of the penial gland of *Deroceras reticulatum* takes 75 minutes according to Nicholas (1984) and "several hours" according to Webb (1961), but it might well take more time in species with more highly branched or longer penial glands.

There is some controversy about the fate of the sperm after penis retraction. Because the sperm is transfered during copulation onto the penis, immediately after retraction it must lie somewhere in the main penial bag (Nicholas 1984, Benke 2006, Reise *et al.* 2007. It must then move via the atrium towards the bursa copulatrix and oviduct. However, there is an array of opinions, some better supported than others, about how long the ejaculate remains in the penis, whether the sperm has to enter the bursa copulatrix or not before proceeding to a sperm storage site, and whether it migrates along the female or male groove of the spermoviduct (Webb 1961 Sirgel 1973, Nicholas 1984, Tompa 1984, Rymzhanov and Schileyko 1991, Wiktor 2000).

DISCUSSION

Despite the mixed quality of observations and the small proportion of species examined, considerable variation in the mating behavior of *Deroceras* is already apparent. However, the extent to which this variation is intraspecific or interspecific is not always clear, and there is a need to investigate the intraspecific variation between and within populations. The genus contains many nominate species of similar morphology; mating behavior can sometimes provide a suite of extra characters to help resolve such taxonomic problems. Because mating behavior is a potential isolating mechanism, it will also be interesting to study mating behavior across the contact zones of closely related species with parapatric distributions.

Mating in *Deroceras* involves very complex copulatory organs and behavioral patterns. After a comparatively long time of caressing with the sarcobela, copulation usually begins very suddenly and sperm transfer occurs often, or maybe always, at the very beginning of copulation. This demands perfect coordination and penis alignment between the partners. It seems plausible that slight discrepancies in the preceding courtship phase (*e.g.*, due to different shape and movement of the sarcobelum) or during sperm transfer (*e.g.*, due to shape differences of the penes and thus less perfect entwining) can impair sperm exchange. I have often observed difficulties between conspecific mating partners from different populations, which might be caused by such slight differences (Reise 2001, unpubl. obs.). In other taxa, intraspecific variation of sexual behavior among populations is common, and morphological, behavioral, and other traits that determine mate recognition (*e.g.*, pheromones) may evolve quickly and play a significant role in allopatric speciation (Arnquist and Danielsson 1999, Verell 1999). If, as hypothesized in the introduction, sexual conflict between mating partners drives rapid evolution of penial morphology and mating behavior in *Deroceras*, interpopulation incompatibilities, rapid speciation, and many species might be the consequence.

There is so far little evidence addressing the importance of sexual conflict in *Deroceras*. The unusual behavior of sperm donors in rare cases of unilateral sperm transfer in *D. rodnae* (see section on copulation) might be interpreted as a preference for the female (sperm receiving) role and for occasional cheating in a mating system based on reciprocity (according to the hermaphrodite's dilemma model: Leonard

1990, 1991, 2005). Both the preference and the cheating suggest partner conflict over sexual roles. However, the cases of unilateral sperm transfer when both ejaculates had been produced might represent sperm rejection, *i.e.* preference of the male role. The preference for one of the two sexual roles has been repeatedly predicted for mating systems of simultaneous hermaphrodites, but it is controversial which factors should decide the preferred role (reviewed by Anthes *et al.* [2006]).

Michiels (1998) has suggested that a preference for the female role could result in elaborate behavior to stimulate the partner into donating sperm and to assess its readiness to do so; until reciprocity is assured, no sperm should be donated. Although we know almost nothing of the mechanisms of stimulation or assessment, this might explain the very long courtships in *Deroceras* and some species of *Limax* Linnaeus, 1758 (Gerhardt 1933), which surely entail higher costs than short courtships (Baur 1998). Assurance of reciprocity and/or manipulation of the mating partner into accepting sperm have been proposed as an explanation of elaborate courtship in a nudibranch (Karlsson and Haase 2002). A further possibility is that the length and vigor of courtship have been sexually selected as honest signals of the partner's condition and thus of its genetic quality. Although complete mate rejection seems to be rare once courtship has started, "weak" courtship behavior might make it more likely that sperm exchange is unilateral, or might reduce how much sperm is donated or the partner's use of donated sperm.

The length of courtship contrasts with the extremely fast penis eversion and sperm transfer in some species of *Deroceras*. Tight physical contact of penes during copulation might ensure reciprocal sperm exchange (*cf.* the entwined penes in *Limax*; Michiels 1998). However, a possible consequence of the rapidity of copulation is that once an individual has everted its sperm mass with its penis, it may have no chance to withhold its ejaculate, should it realize that the partner is not going to donate. This conflicts with Davison *et al.*'s (2005) assumption that in systems with simultaneous reciprocal mating, cheating is possible only after intromission (meaning sperm transfer). The ability to cheat before sperm exchange might be a peculiarity of groups with external penis-to-penis sperm transfer. It remains unclear what has favored the evolution of the rapid penis eversion and sperm transfer; the advantage of being slightly quicker to evert than the partner seems unlikely to be in unilaterally snatching the partner's ejaculate, because the penis has to be fully everted before the ejaculate becomes available. It seems more compatible with a preference for the sperm-donating role.

Another possible cause of partner conflict, widely assumed to exist in gonochorists as well as hermaphrodites,

concerns control over fertilization. Sperm donors should endeavor to ensure that their sperm fertilizes the partner's eggs. If the manipulations to achieve this, or the loss of control itself, involve a cost to the sperm receiver, counteradaptations are expected. In *Deroceras* the most promising evidence of a manipulation comes from the appending penial gland in species in which it is everted only after sperm exchange. This cannot serve sperm exchange but might manipulate the partner into using the donor's sperm, as do allohormones transferred by the love dart of *Cornu aspersum* (see section on copulation). However, other functions are also possible, such as increasing the number of eggs available for fertilization as might be the case in *Lymnaea stagnalis* (Linnaeus, 1758) (Koene *et al.* 2006) or delaying subsequent mating by an antiaphrodisiac effect (*cf.* Andersson *et al.* 2004), or marking the partner so as to prevent repeated mating with the same mate (*cf.* Ivy *et al.* 2005).

The unusual external mode of sperm exchange could also indicate sexual conflict over control of egg fertilization: Emberton (1994) hypothesized that the extremely prolonged intertwining of penes of some polygyrid and *Limax* species represent male efforts to place the ejaculate as far away from the partner's gametolytic bursa copulatrix as possible. The evolution from penis intromission into the bursa trunk towards external transfer from penis to penis has evolved at least four times independently within the pulmonates (Emberton 1994). However, Solem (1974) thought that elaborate genital structures, including very prolonged penes, evolved to enhance species recognition—that is, as an isolation mechanism. I tend to agree with Emberton (1994) and think that circumvention of female control may have driven the abandonment of direct sperm transfer into the bursa copulatrix. However, I do not agree that a longer penis would be even better in circumventing the bursa copulatrix than a moderately long one. Allosperm is believed to travel up the spermoviduct, and thus to pass the entrance of the bursa trunk, irrespective of penis length. Another possible explanation for the very prolonged penes of polygyrids and *Limax* is that they have been sexually selected as condition-dependent cues used to assess the desirability of the mating partner. In contrast, most of the various extravagant penial structures in some *Deroceras* species (Fig. 2) seem unlikely to be reliably condition-dependent (their size is still rather trivial compared with that of the body), but they remain most explicable by some form of arms race.

There are many other aspects of mating behavior and morphology that one might examine to discover indications of partner conflicts in *Deroceras*: the role of the (probably secretion-transferring) sarcobelum, the function of additional penial side pockets (besides ejaculate-holding), the processes occuring after sperm exchange before penis withdrawal, the occasionally long-delayed penis withdrawal in *D.*

sturanyi, and apophallation in Kazakh *D. laeve*. Other suggestions for future research are the study of mating in species that represent morphological or behavioral extremes, and the relating of behavior to morphology in species polymorphic for a penial structure (such as the highly variable sarcobelum in *D. turcicum*: Reise and Hutchinson 2001a). Several other fruitful lines of research depend on the development of a molecular-based phylogeny.

Finally, I will make the following recommendations for studies of mating behavior in *Deroceras*. (i) Observations should include all mating phases, which normally requires introducing individuals to each other in the laboratory. (ii) Records should be kept of matings that cease before copulation, in particular noting at what stage this happens and the size and mating histories of the individuals involved. (iii) Individuals should be followed so as to reveal correlations in which partner takes which role at different stages. (iv) Note whether both partners donate and receive an ejaculate, and, if not, whether both partners have manufactured sperm packages. (v) Direct observations should be complemented by video-recording and rapid killing of couples at successive mating stages. (vi) The studies should include several pairs and, preferably, more than one population.

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