the latter will be aroused and will mount the female laterally. *Stage 3:* subsequently, the male settles on the female's dorsum in a parallel position for a period of 0.5 – 1.0 min, while the female (with the male on her dorsum) will commence walking. *Stage 4:* the male turns his body by ≈180° and transfers his gnathosoma and part of his idiosoma beyond the margin of the female's opisthosoma. The male will then attach himself to the latter by his anal and tarsal suckers. In this position both sexes remain linked for 128 – 219 min, during which the aedeagus is inserted to the bursa copulatrix. Copulatory movements are usually performed for an average period of 30 min. Insemination involves the production and transfer of spermatophores to the receptaculum seminis of the female; this process has been described in detail [4,5].

The events of stage 1 suggest the involvement of a male-produced pheromone causing the recognition of males by the females, while the events of stages 2 and 3 indicate the utilization of a female-produced pheromone which elicits mating activity in the males. The use of sex pheromones for mate finding appears particularly important for *A. siro,* as this species lacks the capability of visual perception.

The above results were corroborated by the observed attractiveness of an extract of male *A. siro* for conspecific females as well as the sexual stimulation of male flour mites by an extract of female *A. siro.* Figure 1a reveals that 0.1 – 5 equivalents of male extract elicit 1.8 – 2.3 female visits, 10 and 25 equivalents of male extract cause 8.5 and 11.5 female visits, while 50 equivalents of this extract subdue female attraction to 2 visits only (partial adaptation). However, the extract of female flour mites failed to attract female *A. siro* when exposed to levels ranging from 0.1 to 50 equivalents (Fig. 1a). Remarkably enough, the duration of female visits on controls (which had been treated by the solvent only) usually took 0.1 – 0.25 min, while it lasted 1.4 – 3.4 min in the presence of 1 – 25 equivalents of male extract. The above visits were cut short, because sexually mature males were not available.

Both visiting frequency and mating attempts of male flour mites depend on the available dosage of the extract of female *A. siro.* The behavior threshold of mating attempts was found to be approximately 10 times lower ($\approx 10^{-6}$ equivalents) in response to female extract than the behavior threshold of visiting frequency ($\approx 10^{-5}$ equivalents). Figure 1b shows that 10^{-4} equivalents of female extract caused ≈1.4 mating attempts and ≈1.7 visits of male *A. siro.* At 10^{-1} and 10^{0} equivalents of female extract, ≈4.0 and 10.8 visits as well as ≈3.2 and 3.8 mating attempts, were respectively induced. A dosage of 10 equivalents of female extract reduced the number of mating attempts to 1.2 and failed to suppress the number of visits (10.2), while 50 equivalents of female extract abolished both visits and mating attempts. The marked drop in the response of male flour mites may be due to their adaptation to overdosed pheromone (Fig. 1b).

The mating attempts of male *A. siro* being evoked by an extract of conspecific females closely resemble stages 2, 3, and 4 of the behavior sequence elicited by sexually mature females. However, the main difference between the former and the latter is the considerably shorter duration of stage 4 (2.4 – 4.8 min) in males stimulated by female extract. This is most likely due to lack of the tactile stimuli being provided by female *A. siro.*

It may be concluded that mutual sex recognition, courtship, and mating of *Acarus siro* L. are mediated by two different sex pheromones: a male-produced attractant and arrestant for virgin females and a female-produced attractant and copulatory stimulant for *un*mated males. These findings could certainly be utilized as parameters of a bioassay for the identification of the molecular structures of the sex pheromones discovered in male and female flour mites.

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Reproductive Dominance Controlled by Mutilation in the Queenless Ant *Diacamma australe*

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Ant queens and workers are morphologically specialized to perform different functions, and this dimorphism is the basis for reproductive division of labour within colonies. However, in a small number of primitive ants (subfamily Ponerinae), the queens have disappeared, and mated workers ("gamergates") reproduce instead [1]. All workers are capable of mating and laying eggs, but only some become the functional reproductives in each colony. There appear to be a variety of patterns to the division of labour in worker societies. In several species many gamergates coexist in a colony [2,3], because all workers which are able to mate during the period of male activity reproduce. In this case there is neither social control over the event of mating nor inhibition of ovarian activity, and insemination alone controls re-

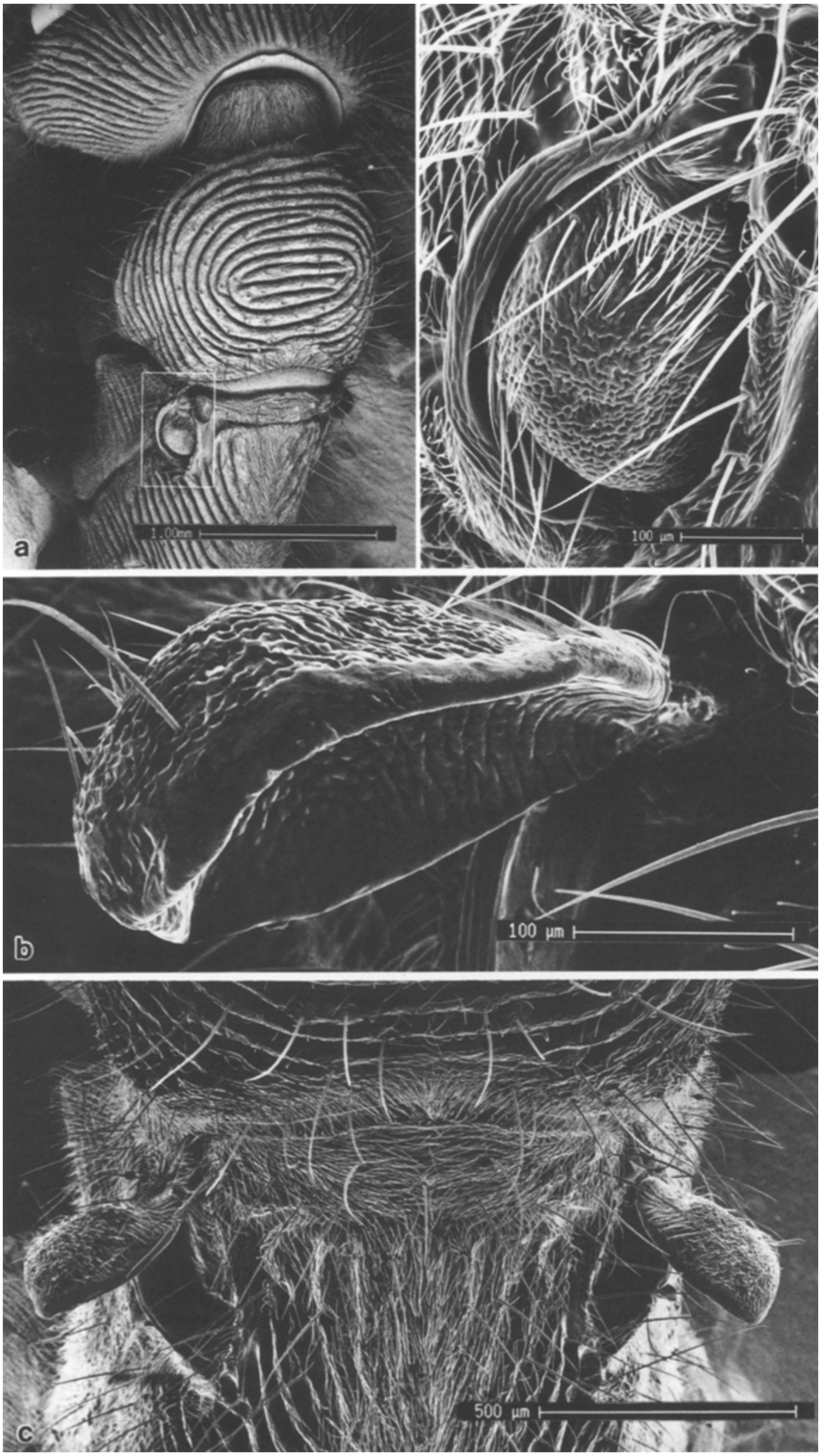

Fig. 1. Scanning electron micrographs of the thoracic appendages in *D. australe.* a) One of the appendages in its normal resting position inside the pleural cavity – the cuticle is elaborately sculptured; b) and c) mutilation can only occur after the single pair of appendages have been folded out of the pleural cavity

productive differentiation amongst colony members [2]. In contrast, only one gamergate occurs in the colonies of the ponerine *Pachycondyla krugeri,* although the regulation of this monogynous condition has not been elucidated [4]. We investigated the phenomenon of reproductive competition among workers in *Diacamma australe,* in which queens are also absent (e.g., *D. rugosum* [5]). This is the first description of a mechanism of social control over mating in worker societies.

Workers of *Diacamma* are unique among ants because they eclose from the cocoon with a pair of bladder-like appendages on the thorax. The term "vestigial wings" has been used to describe these tiny immovable appendages [6], but it is misleading because these highly modified structures bear very little resemblance to wings (Fig. 1).

Nine colonies of *D. australe* were collected near Townsville, north Queensland, in November 1987. Only one worker with thoracic appendages was present in each colony (mean colony size was 129 workers; s.d. 56); a single worker with intact appendages has also been found in the colonies of *D. rugosum* (T. Abe, pers. comm.). Dissection revealed that their spermathecae were full of sperm and they had functional ovaries. The presence of basal inclusions of yellow bodies (which originate from degenerating nurse cells [7]) in the ovaries was taken as further evidence that eggs had been laid. Workers without thoracic appendages were all unmated ($n = 144$; Table 1). Therefore gamergates in *D. australe* can be externally recognized by the retention of the thoracic appendages. With the gamergate present, the workers in colony A (Table 1) all had undeveloped ovaries, except for two individuals with developed ovaries that were much shorter and contained fewer oocytes than those of gamergates. Faint yellow bodies occurred in one of these workers, and it is possible that she laid unfertilized eggs in the presence of the gamergate.

To investigate whether the unmated workers are inhibited from laying eggs, the gamergate was removed in four colonies. Many eggs were soon laid in each colony, and these developed into males. The workers were dissected in one of

Table 1. Reproductive status of mutilated workers from two experimental colonies (with and without a gamergate). Functional ovaries had large yolky oocytes at the base of most ovarioles, and smaller partly yolky oocytes with alternating nurse cells in the distal ends. In colony (I), the gamergate was killed 2 weeks prior to dissections

	Number of workers in field colony	Workers dissected	Workers with undeveloped ovaries	Workers with functional ovaries	Examined workers with empty spermathecae [%]
Gamergate present (A)	139	121	119	2	100 ($n = 98$)
Gamergate removed (I)	82	69	32	37	100 ($n = 46$)

Table 2. Fate of 225 workers of *D. australe* that eclosed in the presence and absence of a gamergate. Discarded cocoons were counted everyday in each nest

	Colony code	Number of cocoons eclosed	Number of callows mutilated
Gamergate present	(F)	41	all
	(G)	14	all
	(H)	14	all
Gamergate absent	(C)	15[a]	all but one
	(E1)	70	all but one
	(F1)	58	all but one
	(F2)	13	all but one

[a]Another 90 cocoons containing males eclosed later

these orphaned colonies [(I); Table 1], and 54% had active ovaries (yellow bodies were conspicuous in gamergates, but absent in recently orphaned workers with active ovaries, possibly because yellow bodies may only become visible after a certain number of eggs have been laid). Thus the single gamergate is able to inhibit the egg production of almost all of her nestmates.

All newly eclosed ("callow") workers of *D. australe* had thoracic appendages, but these were soon severed by the gamergate (three colonies; Table 2). Callow workers were easily distinguishable for several days because their limb extremities are light-brown, and their exoskeleton is soft. Callows attract much attention within a nest following their emergence from cocoons. Typically, a few workers (2–4) grasp the limbs and other body parts of the callows while additional workers groom them and remove the larval skin. During this exercise the gamergate intermittently licks and scrapes the dorsal trunk region, and clearly attempts to remove the thoracic appendages. First these need to be folded out of the pleural cavity (Fig. 1), and then they can be pulled off. It is an erratic process, and can take several hours before a newly eclosed worker is mutilated, especially when many cocoons eclose at the same time (usually 2–3 per day, never more than 6 per day). Callow workers often resist and try to escape, and mutilation is possible only because they are held captive by other workers. However, there is no active complicity from these workers, and only the gamergate mutilates callows.

Are callow workers mutilated in colonies without a gamergate? Workers eclosed in four experimental colonies from which we had recently removed the gamergate (i.e., the gamergate was their mother) (Table 2), and the older workers did not attempt to mutilate them. However, one of the callow workers (usually the oldest) in each colony soon proceeded to systematically mutilate all the workers which subsequently eclosed. If this unmutilated callow was taken away, a younger callow was then able to keep her thoracic appendages. The mutilated callow workers were characteristically timid and inactive within the nests, but unmutilated callows were very active and behaved aggressively. They persistently harassed older workers (sudden lunge, bite limbs or antennae, violent jerking). The unmutilated workers in the various colonies soon began to lay eggs, and on several occasions ate eggs laid by the mutilated workers.

Adult males were reared in one of the orphaned colonies (C). Once these males attempted to fly out of the experimental cages, we introduced them in other orphaned groups of workers (each with an unmutilated individual). These foreign males were soon carried inside the nests by workers. All observed copulations ($n = 4$) involved unmutilated workers only. Dissection confirmed that these four unmutilated workers had been inseminated, and not others.

We have documented in *D. australe* a pattern of reproductive control which occurs in two distinct social contexts: (1) in established colonies, the single gamergate maintains her supremacy by inhibiting the other workers from producing males, and by mutilating all young workers (thus preventing them from being inseminated by foreign males); (2) after the gamergate disappears (following her natural death or fortuitous budding of an existing colony), a newly eclosed worker will mutilate others in her age cohort. As a result, she is the only individual to mate when males visit, and she then becomes the new gamergate. Furthermore, while she is unmated, the unmutilated worker aggressively restricts the production of eggs by her nestmates.

The physiological basis for the reproductive supremacy seen in *D. australe* remains to be determined. Mutilation affects the behavior of young workers, and also determines whether males will mate with them. We hypothesize that mutilation of the thoracic appendages has an effect on the production of sexual attractants in the pygidial gland [8]. After mating, the gamergate is able to control the ovarian activity of her nestmates without physical harassment, which suggests that inhibition then becomes pheromonal in nature. This is an interesting parallel to *Apis capensis,* where laying workers in orphaned groups produce a primer pheromone which is similar to the queen's [9].

In ants there are a variety of mechanisms which regulate the number of queens per colony [10]. In this context the lack of social control over reproduction in some queenless species [2,3] is intriguing. However, monogyny has now been demonstrated in *Pachycondyla krugeri* [4] and *D. australe,* and in both species the single gamergate inhibits the ovarian activity of unmated workers. Furthermore, in *D. australe,* the possession of thoracic appendages has led to the evolution of a unique mechanism of reproductive dominance, whereby the gamergate prevents nestmates from mating.

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Naturwissenschaften Buchbesprechungen

Trinkwasser. Untersuchung und Beurteilung von Trink- und Schwimmbadwasser. Von K.-E. Quentin unter Mitarbeit von I. Alexander und D. Eichelsdörfer. Berlin-Heidelberg-New York: Springer 1988. XX, 385 S., 47 Abb., DM 280,–.

Das Buch soll die Tradition des schon vor über 80 Jahren, also in einer Zeit, in der Umweltprobleme noch weitgehend unbekannt waren, im Springer-Verlag erschienenen Buches von Klut „Untersuchung des Wassers an Ort und Stelle" fortsetzen. Jenes handliche, praxisorientierte Buch erlebte bis 1945 neun Auflagen. Es wurde seit der 8. Auflage substantiell wesentlich erweitert durch die Überarbeitung von Olszewski (Autor: mit *i* und nicht *y* am Ende!), der den Titel erweiterte um: „...seine Beurteilung und Aufbereitung". Dies machte auch den besonderen Wert jenes Buches aus: Da gab ein Praktiker (Olszewski war Laboratoriumsleiter bei den Dresdener Wasserwerken) seine Erfahrungen zu Wasserbeurteilungen preis.

In der Beurteilung liegt auch der Schwerpunkt der Neuerscheinung. Für die Analysenmethoden selbst gibt es ja die universell angewandten Deutschen Einheitsverfahren zur Wasser-, Abwasser- und Schlammuntersuchung, die nunmehr in ihrer dritten – als Loseblattwerk erstellten – Auflage durch die in rascher Folge erscheinenden Lieferungen auf dem neuesten Stand gehalten wird. Heute füllen die zahlreichen, von einem großen Mitarbeiterstab aus der Fachgruppe Wasserchemie der GDCh ausgearbeiteten und durch Ringversuche vielseitig getesteten Verfahren schon einige Bände. Die meisten dieser Verfahren sind inzwischen DIN-Normen, und teilweise finden sie sogar Eingang in die ISO.

Es ist schon mutig, trotz dieser ungeheuren Materialsammlung ein Buch zum Thema Trinkwasseranalytik zu publizieren; doch dieser Versuch hat sich gelohnt, denn hier ist ein handliches und dennoch inhaltsreiches Buch entstanden, das rasch und übersichtlich eine Orientierung über die vielfältigen Möglichkeiten der Wasseranalytik, die Anforderungen und Bewertung der Ergebnisse bietet. Es ist ein Lehr- und Nachschlagebuch zur Wasseranalytik, während die Deutschen Einheitsverfahren die detaillierten Arbeitsvorschriften bewährter und abgesicherter Verfahren bietet, deren Ergebnisse „justitiabel" sind, also zu Ergebnissen führen, die gerichtlichen Prüfungen standhalten. Leider vermißt man in dem zu besprechenden Buch einen Hinweis auf diese Einheitsverfahren, deren Bedeutung schon einen eigenen kleinen Abschnitt rechtfertigen würde. So sind nur bei den einzelnen Verfahren Literaturhinweise auf diese Arbeitsvorschriften und die darauf beruhenden DIN-Normen gegeben.

Was diesen Band besonders auszeichnet, ist die Darstellung der für die Beurteilung der Trinkwasserbeschaffenheit maßgeblichen Gesetze, Verordnungen, Richtlinien und auch von Grenzwerten, sogar aus dem internationalen Bereich (WHO, USEPA). Besonders nützlich sind die Abschnitte „Beurteilung und

