

The sexual behaviour of some longhorned beetles (Col., Cerambycidae).

By

Axel Michelsen

Zoophysiological Laboratory A,
32, Juliane Mariesvej, Copenhagen Ø.

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Introduction.

The sexual behaviour of longhorned beetles has been reviewed by Butovitsch (1939) and Linsley (1959 and 1961), and a comparative study of 16 species has been published for the subfamily Lepturinae (Michelsen, 1963). The tactile, stimulatory actions of the male have been described elsewhere (Michelsen, 1966). The present investigation comprises recent studies on some Lepturinae, a description of the sexual and fighting behaviour in the subfamily Cerambycinae, observations on one species of the subfamily Spondylinae and on two species of the family Chrysomelidae. A comparative analysis is attempted for some parts of the sexual behaviour of the species.

The sexual behaviour.

Recognition of the female.

Most species of the subfamily Lepturinae and some Cerambycinae congregate in sunshine on composite and umbelliferous flowers for feeding. The males seem to recognize the females at a very short distance, in most cases by touching them with the antennae. The effective stimulus is probably a sex-specific odour since the males, with antennae removed, lose interest in the females (Heintze, 1925), and males which have just been in copula are often mounted by other males. The males of a few species (e.g. *Rhagium mordax*) seem to recognize the females by sight at a longer distance.

In the subfamily Cerambycinae the males and females of a number of species (e.g. *Tetropium castaneum*, *Cerambyx cerdo*, *Asemum striatum*) gather on the stems or stumps of the trees in which they breed. When meeting another animal a *Tetropium* male, still at a distance of 1—2 cm, often stops, and his antennae start trembling. If the other animal is a female she may turn around and start running away. Normally the male runs after her and tries to mount her. If the other animal remains immobile, he walks forward to a distance of less than one cm (cf. fighting behaviour, p. 339, and fig. 7) and if it is a male, he will then attack, or, if a female, he will attempt to mount. Probably the first stimulus is visual, whereas the second is a sex-specific odour which occurs in a low concentration relative to the sensitivity of the chemoreceptors. On the antennae of *Tetropium* Schimitschek (1929) found numerous thin-walled setae which he described as chemoreceptors.

The '♀-signal'.

In *Asemum striatum* it was observed a few times that a female meeting a male immediately turned around and ran away, pursued by the male. This was also frequently observed in *Tetropium castaneum* and *Clytus mysticus*. In *Cl. mysticus* probably no sex-specific odour is present, and if the other animal does not move, the male seems unable to distinguish between the sexes. On several occasions it was observed that two males placed side by side with their heads in opposite directions started to run around, each one trying to mount the retreating abdomen of the other male, see

fig. 1. This suggests that for the males of a number of species the sight of a retreating abdomen indicates a female.

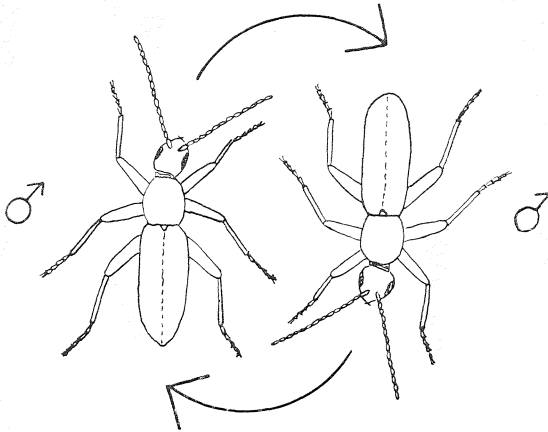


Fig. 1. The '♀-signal' in *Clytus mysticus* (see the text).

A m p l e x u s.

The male usually takes the female without her cooperation and mounts her. In most species she immediately becomes very 'restless', runs about, raises her abdomen, and kicks the male with her hindlegs. Though the male begins to control the female, he often fails at first and is kicked off after a few seconds. During amplexus the males perform a number of actions which have a calming effect upon the female (licking, tapping, scraping, biting of the pronotum or an antenna, abdominal movements, pulling of ovipositor, wiping, striking the abdomen). These actions have been described in detail elsewhere (Michelsen, 1966). The antennal movements performed by the male during stimulation of the female are described below.

C o p u l a.

Contact between the copulatory organs is established in various ways (Michelsen, 1963). In some species the abdominal tips remain together during copula, but in other species the male pulls out the ovipositor of the female. The internal sac of the male may be pulled out when the ovipositor reaches its full length. In some species the ovipositor is then withdrawn into the abdomen of the female, and only the internal sac of the male is visible during

copula. In other species the ovipositor remains visible during copula.

During the first period of copula the females of most species are quiet. In some species the males continue active stimulation of the female, though these stimulatory actions often differ from those of more disturbed periods. In several species however, the male may stop active stimulation, or he may perform the oral action in the air some millimetres above the female body. A similar incomplete stimulatory behaviour is observed in the few species (e.g. *Spondylis*), in which the female is quiet during the whole mating. In some species periods of apparently spontaneous activity of the male has been observed.

End of mating.

In a few species the male leaves the female after some time without previous efforts by the female to dislodge him. In most species, however, the female becomes restless after a period of copulation. The male then usually performs the same stimulatory actions as during amplexus, and in most cases the female becomes quiet. But after a short time the female becomes more and more

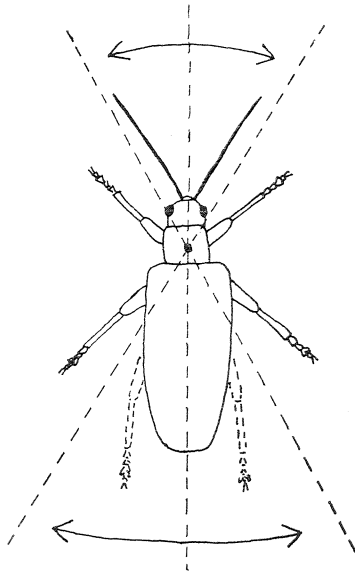


Fig. 2. The 'pendulum movements' in the female *Donacia aquatica* (the male has not been drawn).

restless and finally dislodges the male. In the genus *Rhagium* a 'round dance' is used to throw off the male (Michelsen, 1963). In *Donacia aquatica* the female is very restless after the end of copula and often performs 'pendulum movements', i.e. the female stands upon the front and middle pair of legs, lifts her hindlegs, and turns her body rapidly from side to side like a pendulum centred near the middle of the pronotum (fig. 2).

Antennal movements.

The movements of the antennae of the male in states of excite-

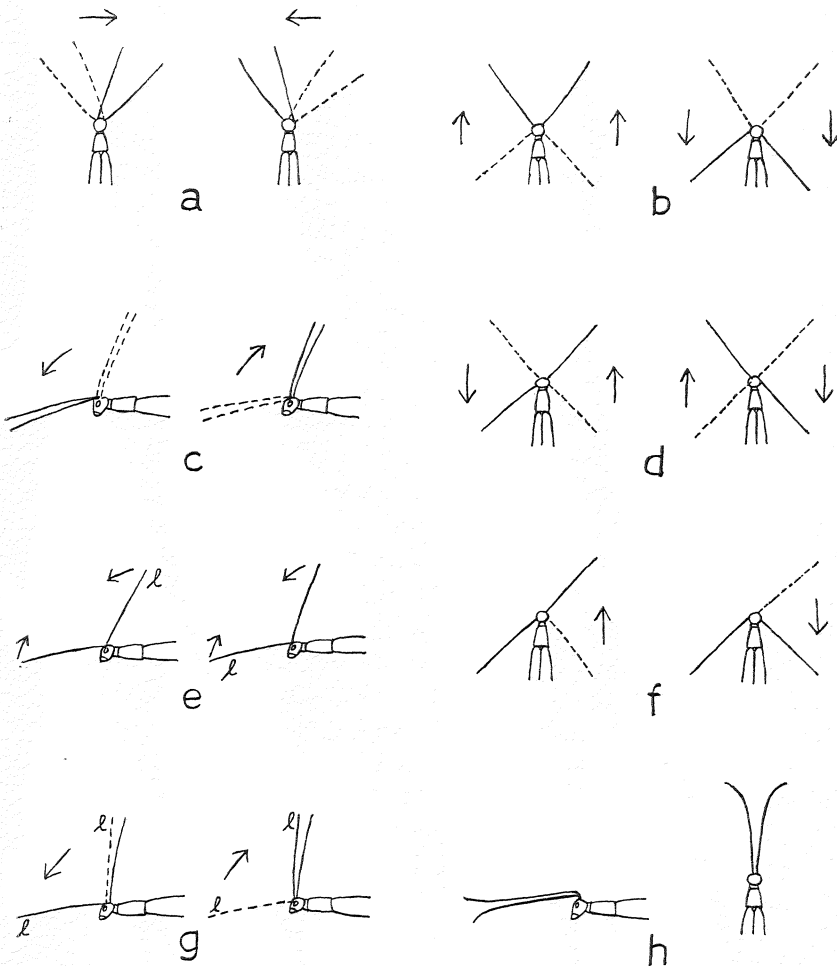


Fig. 3. The types of antennal movements (cf. table 1).

ment seem to be (fundamentally) inherent in the order Coleoptera (Michelsen, 1963). A detailed analysis of the antennal movements is complicated by the interaction of several types in most species. However, it is possible to describe the movements in most species as composed of one or more of the seven types (and one posture) illustrated in fig. 3 and characterized in table 1.

In table 1 'in phase' means that both antennae move together in phase, as opposed to the 'out of phase' type where the antennae are completely out of phase, one beginning to move up/backward, when the other starts to move down/forward. 'Parallel' means that the angle between the two antennae remains (almost) constant during the movement.

Table 1.

Characterization of the simple types of antennal movements in the males (for explanation see the text).

	Types of antennal movements						
	a	b	c	d	e	f	g
Both antennae	+	+	+	+	+	—	—
Horizontal	+	+	—	+	—	+	—
'In phase'	+	+	+	—	—		
'Parallel'	+	—	+	—	—		

The types of antennal movements found in the individual species are given below. As for the species previously investigated (Michelsen, 1963) an examination of ciné films indicated the following types: *Rhagium bifasciatum*: c, e, *Acmaeops collaris*: a-c, f (?), *Gaurotes virginea*: a, e, f (these f strokes were performed with the other (immobile) antenna pointing forward), Donaciinae (*Donacia semicuprea* and *Plateumaris sericea*): a, *Judolia cerambyciformis*: b, d (?), *Strangalia maculata*: d, e, *Strangalia quadri-fasciata*: d-e, g, f, h (not typical), *Strangalia attenuata*: e, g, very weak b, *Leptura rubra*: c, e, circular movements (see Michelsen, 1963), *Leptura sanguinolenta*: c, d, f-g, e, *Leptura maculicornis*: (b), d-e, g, f (?), *Grammoptera tabacicolor*: e, d-e.

Though the antennal movements may be synchronous with the stimulatory actions (observed in *Strangalia attenuata*, *Plagionotus floralis*, *Clytus mysticus*, and *Obrium brunneum*) this is not normally the case. The function of the antennal movements is still unknown. In some other beetles (see Selander, 1964, and

Michelsen, 1963) the antennae may hit the female body, but this has only been observed in *Donacia aquatica*.

Sound production.

It is well known that most cerambycids produce sounds when disturbed (for references see Frings & Frings, 1960, and Linsley, 1959 and 1961) and normally the stridulation has been regarded as defensive. In some species sounds may be produced by undisturbed animals. Several lepturines and cerambycines stridulate during sexual activity. The stridulation of the male is coupled to the tactile stimulation, and normally the sounds are different from those produced when the animal is disturbed. A few examples should be mentioned here:

In *Leptura sexguttata* the males produce a single type of sound (about 90 chirps/min.) during the tapping action. The male of *Leptura rubra* may stridulate in two ways (which are discernible by the human ear): The sound produced at the establishment of mating and when the female is restless resembles the 'protest sound' produced when the animal is disturbed. During the fast tapping action another type of sound is produced synchronous to the tapping.

In *Clytus arietis* the female may stridulate during the establishment of amplexus, and both sexes produce rhythmical 'squeaking' sounds (which seem different to the human ear) during copula. In *Clytus mysticus* loud sounds are produced by the male during copula. The sound production is rhythmical and synchronous with the licking, tapping, and abdominal movements. At the end of copula the female may stridulate. In *Plagionotus floralis* also, both sexes may stridulate during mating. When the female is restless, the male often stridulates, licks, and moves his antennae.

Significance of the tactile stimuli.

The stimulatory actions performed by the male seem to have a calming effect upon the female: a restless female becomes quiet when the male starts to stimulate her. If the male stops the stimulatory action, the female may again become restless, the male again starts to stimulate her, and so on. In the male the stimulatory actions and the antennal movements appear to be released by movements of the female (kicks, restless behaviour) or some other disturbance (e.g. pushing of the male with a pair of forceps).

In the female, actions similar to the restless behaviour can be observed if a piece of plasticine is placed upon the back of a female.

It is not known whether the variations in stimulatory behaviour together with the restless behaviour of the female play a role as an isolating mechanism operating at species level. Although a few observations of inter-species attempts at mating can be found in the literature, this seems to be a rather rare phenomenon.

For most species it is very difficult to distinguish the factors releasing the behaviour of the two sexes during mating, especially during the first period of copula. However, a comparison of the alternative behaviour patterns shown by *Strangalia bifasciata* during copula sheds some light upon these questions:

Type 1. During copula the male may remain on the back of the female, his licking and tapping changing into a pure tapping performed in the air some millimetres above the scutellum of the female. After some time the female becomes restless and kicks and finally throws off the male, which licks her scutellum whilst moving his antennae.

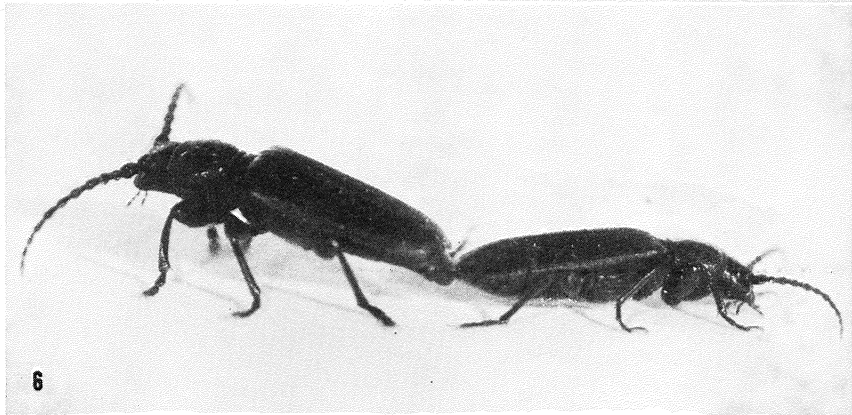
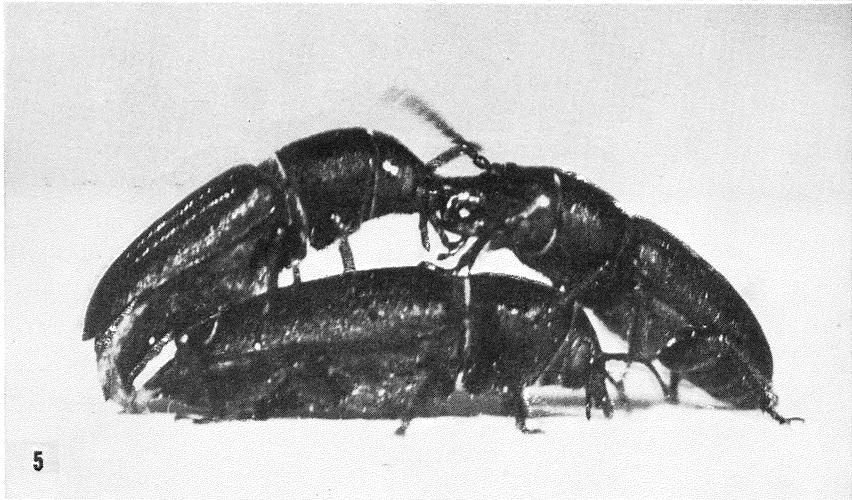
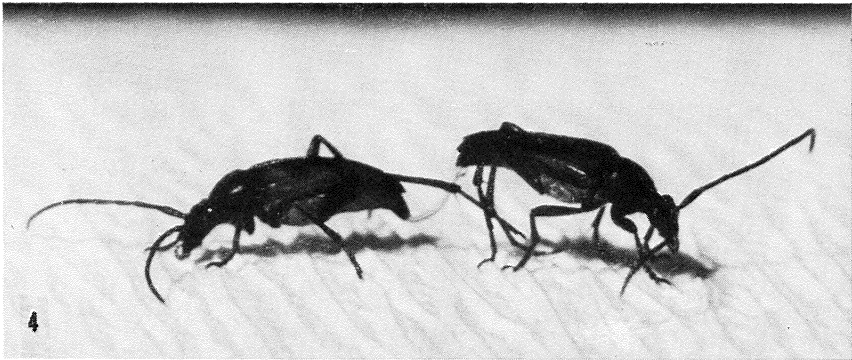
Type 2. The male leaves the female for a position in line with her facing in the opposite direction (fig. 4), and stays in this position during the rest of mating. The male now performs the tapping action in the air, often synchronous with penis movements. After some time the female walks forwards, and sooner or later the genital organs are pulled apart.

A male may copulate in both ways in different matings. The fact that tapping in the air also occurs in type (2), i.e. without the presence of a female under the male, suggests that a 'calm period licking or tapping' should be distinguished from the licking or tapping released together with movements of the antennae by a disturbance. In type (2) neither stimulatory behaviour nor antennal movements are seen when the copulatory organs are pulled apart. This might suggest that the stimulatory behaviour induced by a disturbance depends on the presence of a female under the male.

Fig. 4. The position of *Strangalia bifasciata* during copula, type 2.

Fig. 5. A male *Spondylis buprestoides* attempting to push the copulating male down from the female's back.

Fig. 6. A typical position of *Tetropium castaneum* during copula.



The females in type (1) are restless and kick the males at the end of copula (as in a typical lepturine mating), but females in type (2) behave more like a female a leg of which has been fastened to the substratum, i.e. just pulling until the genital organs separate. These observations and the experiments with burdens on the female's back suggest that the restless behaviour of the female—normally inhibited by the stimulatory actions of the male—is induced by the presence of 'something' upon her back and not directly dependent on sexual behaviour.

Fighting behaviour.

Especially in the subfamily Cerambycinae the males of several species compete for the females. In some species (e.g. *Clytus arietis*, *Spondylis buprestoides*) a male may attempt to mount a female already in copula, pushing the copulating male down from the female's back (fig. 5). In *Rhagium bifasciatum* (Lepturinae) a male may try to pull down a copulating male by grasping its antennae with the mouthparts (Michelsen, 1963). In these species the copulating male does not defend itself against the aggressor, but in several species real fights occur.

1. *Asemum striatum* L.

Males may be attacked by others especially during copula. In some cases the copulating male does not defend itself, but usually the two animals fight, each trying to bite off legs or antennae. Both males may lose several appendages in these fights, e.g. one male had only one and a half legs and half an antenna left, when he stopped his aggression against a copulating male. In general these fights seem to be rather primitive without any stereotyped pattern of reactions.

2. *Tetropium castaneum* L.

The fighting behaviour of this species has developed into a pattern of reactions, which appears to be very stereotyped. The fighting normally consists of a sudden leap against the other animal with the mandibles outspread. Usually one of the animals retires, but real biting may occur. Normally the animals do not lose as great a number of appendages as do *Asemum* males. Copulating males which have been attacked by another male for some time may grasp the aggressor, raise it into the air, shake it for some time and finally drop it. Following this the aggressor normally tries to escape!

As described on p. 345 (fig. 6) the male often leaves the female's back during copula. When a strange male approaches a pair in copula, the male rapidly leaves his position on the female's back and faces the intruder. If the stranger runs around the pair, the copulating male turns so as to face him. When disturbed the female often runs forward, the male being drawn with her (cf. the behaviour of *Pyrota*, Selander, 1964). Sometimes when he is not able to walk backward rapidly enough the female just pulls him along.

When in copula the male is inclined to attack all animals which come near. Apparently, the copulating male attacks the other animal first and then during the attack it determines whether the other was really a male. If that was the case the attack continues until the other male has been driven away. If however, the stranger appears to be a female, the male may suddenly stop his attack, leave his mate, and try to mount the new female. The stimuli from females coming along apparently are stronger than

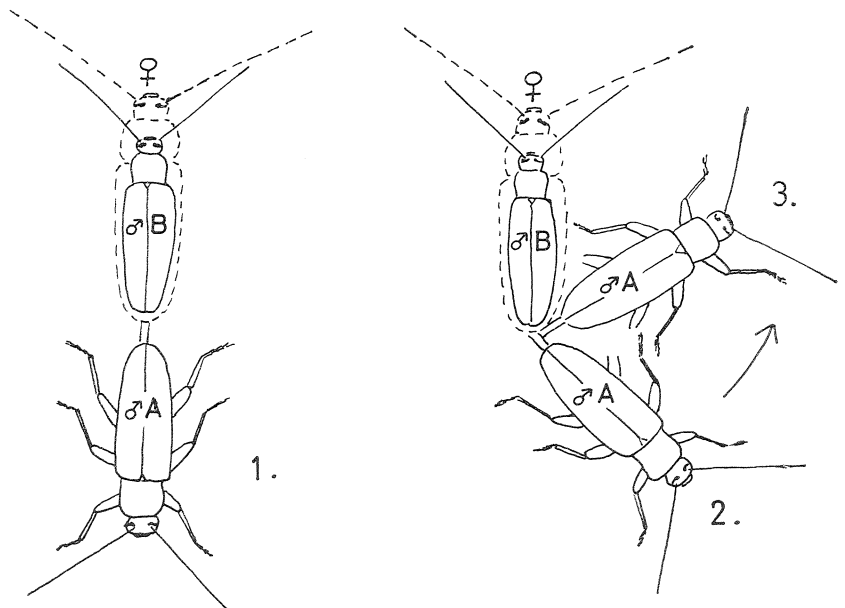


Fig. 7. *Tetropium castaneum*. 1. A strange male (B) has mounted the copulating female, apparently unnoticed by the male (A). 2. The male (A) moves towards his position on the back of the female, but does not attack the stranger (B). 3. When his antennae are about 1 cm from it, the attack begins.

the stimuli of the copulation for a male not situated on the back of a female. The reason a *Tetropium* male in copula, standing askew relative to the female, does not show the same strong tendency to mount the female may be due to the absence of the '♀-signal', i.e. the moving female abdomen (see p. 330). Further observations on this problem are necessary.

When a strange male is driven away by a copulating male, it often walks backwards until it is some centimetres from the copulating male. It then runs in a circle towards the female, mounts her, and starts to stimulate her (fig. 7: 1). It also happens that a strange male approaches the pair from a side not defended by the copulating male enabling it to mount the female without being attacked. Though still in copula with the female, the male does not notice the intruding male, which may stay on the back of the female for several minutes (fig. 7: 1 & 2). Occasionally the male moves from his position on the substratum to the normal position on the back of the female. When the distance from the antennae of the male to the body of the strange male thus becomes less than one cm (fig. 7: 3) the male suddenly attacks the strange male and drives it away. This observation supports the conclusion from the recognition behaviour (p. 330) that a male determines the sex of another animal by means of chemoreceptors on the antennae.

During the observations of the fighting behaviour of *Tetropium* males, which were known individually, it appeared that some males were more likely to win their fights than others. But the existence of a 'dominance system', which is also made probable by the observations on *Cerambyx cerdo* described below, has not yet been demonstrated.

In nature *Tetropium* often emerges in great numbers from a few stumps or trees. Several adults may be found together, running about upon the same stump or hiding themselves in crevices of the bark. Although the behaviour of these animals has not been studied in nature, they are known to occur in such great densities that the fighting behaviour is probably an important part of their biology. Schimitschek (1929) studied the closely related species *Tetropium gabrieli* Weise in nature and found that it mates in the day time, hiding itself during the night. Mating is observed a few hours after hatching, and several copulations are

necessary to fertilize the eggs. This species is known to copulate in crevices in the bark (Crawshay, 1907).

3. *Cerambyx scopoli* Füssl. (*cerdo* Scop.).

The female of this species is rather pugnacious. When a male and female meet each other face to face the male may often be attacked and bitten by the female. If during the mating the pair falls down or the male leaves his position on the back of the female, she may also attack him. A strange male approaching a pair may be attacked by both the male and the female.

In captivity a struggle between two males is the most common type of fight observed. The males bite each other at the base of an antenna and push the body of the other male backwards. Due to the strong cuticula of the basal segments of the antennae the animals normally do not injure each other. After a fight the participants are very restless and one of them may try to mate with another male, a new fight resulting.

Nothing is known about the importance of fighting behaviour in nature. These animals often meet and mate on flowers, and probably it is seldom that several males meet each other at the same spot (cf. *Tetropium* and *C. cerdo*).

4. *Cerambyx cerdo* L. (*heros* Scop.).

Döhring (1949) observed seven cases of fights between males in nature. I have observed numerous fights between animals in the laboratory. Allowing for their greater size the two *Cerambyx* species sense each other at a smaller distance (3-5 cm) than do *Tetropium* males.

Normally one of the males grasps an antenna or a leg of the other male with its mouthparts. It then pushes the other male backwards, and sometimes raises it into the air, shaking it violently. Normally, the weaker male produces sounds when grasped and runs away after the fight.

In one case a great battle between two males was observed. First one of them bit an antenna of the other. After a minute it released its grasp and the two males again attacked each other. When one of the males had been bitten by the other, it stood still until the other released its grasp. During this period the biting male often suddenly sprang against the other, pushing it backwards. The two males continued the fight for about twenty minutes, exchanging about a dozen bites.

Five males were observed during four hours with no females present. It appeared that two of the males were more inclined to bite than the others. Further, when bitten by one of these two males the other males in most cases ran away if the animals met again. When a female was placed in the cage one of the stronger males mated her without being disturbed by the weaker males. On the other hand, when one of the weaker males was mating it might be attacked by one of the stronger males, bitten and pushed down from the back of the female.

In nature Döhning (1949) found that matings and fights take place on a rather limited area of the stem of a small group of trees. A female is often present near the fighting males, and after the fight the stronger male might mate with the female. Because of the relatively great density of animals on the trees one might expect the fighting to be important in the selection of males in nature, but further observations are necessary on this point.

5. *Clytus mysticus* L.

In this species probably no sex-specific odour is present, and it seems that the males try to mate with all animals which behave like females, i.e. running away when they meet another animal. In captivity it often happens that a male attempts to mate with another male (cf. the ♀-signal, p. 330), and within a short time the 'female-male' attacks the 'mating' male, each animal biting legs or antennae of the other during the short fight. Nothing is known about the behaviour of this species in nature.

6. Other cerambycides.

Fighting behaviour within the cerambycine subfamily has been described by several authors (Dusham, 1921; Beeson & Bhatia, 1939; Dürr, 1956; Chemsak, 1963), and fighting also occurs in Prioninae (Mjöberg, 1905; Duffy, 1946) and in Lamiinae (Webster, 1904; Neander, 1928; Butovitsch, 1939; Funke, 1957). In most species the males bite each other, but in some lamiine species the males use the antennae or legs as weapons or push each other backwards with their heads.

The sexual behaviour of the species.

The actions common to most species are listed in table 2. The descriptions given below only comprise behaviour patterns not listed in the table and not described above. The behaviour of a

few species is so far removed from the typical that it has not been possible to fit it into the table, and it is therefore described in some detail below.

1. Subfamily *Lepturinae*.

a. *Leptura livida* F.

The antennal movements are performed with the first antennal segment immobile, and they are rather complex, consisting of types g-f, c, and h components. During amplexus and at the end of copula several series of quick single strokes are performed by the two antennae alternately. During copula, however, single strokes may be performed individually (type g) so that one may observe three strokes of the left antenna, two of the right, one left, two right, etc.

b. *Strangalia septempunctata* F.

Antennal movements of type d during amplexus and type b-c at the end of copula.

c. *Strangalia bifasciata* Müll.

The behaviour of this species is remarkable. The mating begins in the usual way: The male mounts the female and licks her scutellum and pronotum during the brief amplexus. No or only a few antennal movements (horizontal 'in phase', type b) are seen. The penis is fastened, with about 5 mm of this organ being visible. A combined licking and tapping upon the scutellum is observed during the first minute. The copula may then continue in two alternative ways as described on p. 336.

d. *Pidonia lurida* F.

Antennal movements of type e and f-g (the first segment immobile). During amplexus a male stroke the female's body with his hindlegs. In some cases mating was attempted between two males.

e. *Grammoptera ruficornis* F.

In this species some remarkable actions are found. Amplexus is rather calm, a few or no antennal movements (type b-c) and occasionally licking are observed. The male antennae are directed backward. After the establishment of copula the male taps, or taps and licks the female.

Suddenly the male becomes restless (without any previous

movements of the female—cf. the behaviour of *Acmaeops collaris* and Donaciinae, Michelsen, 1963) and strikes the sides of the female's abdomen with his hindlegs, moving backward and pulling out the genital organs until they separate (fig. 8). The male then moves forward upon the female, bending his hindlegs around the abdomen of the female, which now has become restless and in most cases throws off the male (cf. the behaviour of *Rhagium mordax*, Michelsen, 1963). No licking or antennal movements are seen.

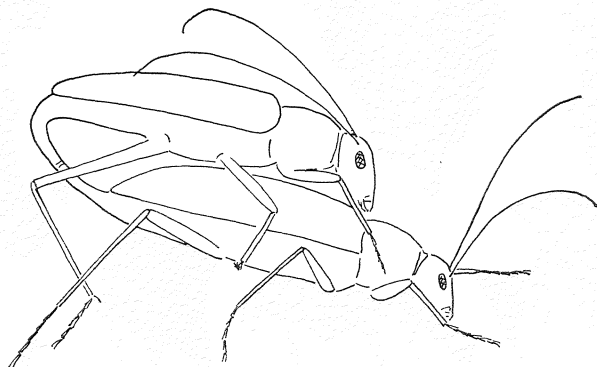


Fig. 8. The pulling of the genital organs at the end of copula in *Grammoptera ruficornis*.

In one case the female was restless during amplexus and the male stroke her abdomen in the same way as in copula. A pair in copula had been placed near a hot photobulb, and the female became restless and kicked the male, which licked her and moved his antennae, i.e. the typical lepturine end of mating behaviour.

2. Subfamily *Cerambycinae*, (including the subfamily *Aseminae* of some classifications).

a. *Asemum striatum* L.

Only few observations were made. Violent antennal movements of type a are seen during amplexus and the periods of copula with a 'spontaneous activity' in the male (see Michelsen, 1963). The male may leave the female's back during copula and face other males.

b. *Tetropium castaneum* L.

The biology of this species has been described by Crawshaw

(1907). The antennal movements (type a) and all other actions in this species are performed very rapidly. This is especially the case in fighting behaviour (see p. 338). During copula the male often leaves his position on the back of the female, enabling him to face aggressors even when in copula (fig. 6). At the end of copula the female may start to run, the genital organs being pulled apart.

c. *Clytus arietis* L.

Antennal movements are of type e. In most cases the female is restless at the end of copula, but in some cases the male leaves the female after a period of calm copula.

d. *Clytus (Anaglyptus) mysticus* L.

Antennal movements are of type d-e, and b. The stimulatory actions are rather variable. During calm periods of copula either licking, tapping, or penis movements may be performed as the only stimulatory action. In most cases, however, they are performed together, being coupled as a synchronous pattern of rhythmical actions. In one male a synchronous coupling between licking, tapping, sound production, penis movements, and antennal movements was observed. During periods of active stimulation the male may perform a *s c r a p i n g* action, i.e. the head is moved backward with the widespread mandibles pressed against the female's back.

During amplexus the scraping action is performed, usually upon the posterior part of the pronotum or the anterior part of the elytra, whereas during the intermediate periods calm licking or licking and tapping actions are performed further back upon the female. During copula a number of short series of scraping actions are performed, alternating with the stimulatory actions described above. At the end of mating scraping may also occur, but some males performed a combined licking and tapping as response to the restless behaviour of the female. Copula may end in the usual way, but a final pulling of the genital organs (cf. *Rhagium mordax*, Michelsen, 1963) has also been observed. The male then moves backward over the female.

e. *Clytus rhamnii* Germ.

Only a single observation on this species. At the end of mating the male merely dismounted and pulled the genital organs apart.

f. *Clytanthus sartor* Müll.

Antennal movements are of type d. During copula the female is periodically restless and kicks the male, which then moves his antennae and performs the scraping action upon the back of the female. However, during most of copula synchronous licking, tapping, and penis movements are observed.

g. *Plagionotus floralis* Pall.

Antennal movements are of types d, b, c, and h. In one male the antennae were bent between the first and second segments during type c movements. Some violent movements in the male resembling the scraping action have also been observed.

h. *Stenopterus rufus* L.

Only two observations were made. Antennal movements are of types c and e. During the beginning and at the end of copula the male bends his body over the back of the female and performs a combined licking and tapping alternating with series of scraping actions. At a later stage of the mating a pure tapping is performed in the air above the female's body.

i. *Obrium brunneum* F.

The mating in this species consists of a series of copulations alternating with short periods of amplexus. The mating lasts from one half to over two hours, and during this time 5 to 10 copulations occur. The antennal movements are of type d-e. Sounds may be produced by the male during the establishment of copula. An attempt at mating between two males has been observed.

j. *Callidium violaceum* L.

After a period of violent stimulation (which resembles the scraping action, but is performed as pure licking) the female extrudes the tip of her ovipositor, which the male pulls out to establish copula. During copula the penis and the ovipositor form a bridge between the two abdomens, which are moved by rhythmical abdominal actions coupled to the tapping. The stimulation during periods of 'spontaneous activity', at the end of copula, and during the post-copulatory amplexus, is similar to that seen during the precopulatory amplexus.

k. *Phymatodes testaceus* L.

The antennal movements of type a-d are very weak. The rhythmic pulling of the ovipositor is coupled to the tapping action, but

initially these actions are not synchronous with the licking action. The male strikes the abdomen of the female with his tibial spurs during amplexus and at the end of copula.

l. *Cerambyx scopoli* Füssl. (*cerdo* Scop.).

During each mating several copulations occur, separated by period of amplexus. The stimulatory actions are often very violent, the scraping action being combined with a biting of the pronotum of the female, but licking has also been observed. During amplexus antennal movements of types a and b occur, and the h position is often observed (cf. *Cerambyx cerdo*). In one case the female produced sounds during the establishment of copula. The first part of copula is quiet, with weak tapping and abdominal actions being performed by the male. But later, a series of biting and scraping actions may occur.

m. *Cerambyx cerdo* L. (*heros* Scop.).

The biology of this species has been studied by several authors. Döhring (1949) investigated the sexual behaviour very carefully and related it to the anatomy of the genital organs. Her observations have been confirmed here. The behaviour is characterized by the quiescent female and the large number (often more than 10) of copulations during each mating, which lasts about one hour. The antennal movements are generally of type a, but the h position is often observed during the establishment of copula.

During the establishment of copula a pure licking is observed, and often synchronous movements of the mandibles are seen. Frequently the male takes up a position further back upon the female during active stimulation than during quiet periods, and sounds are often produced. Normally the female is quiet but Döhring observed that some females kicked the male when he attempted copula. During the first part of copula the ovipositor and the internal sac form a bridge between the two abdomens which are pulled and relaxed by the rhythmical abdominal movements. These are synchronous with a few tapping actions performed in the air above the female's back. Döhring suggests that these movements are necessary for the transfer of semen. After a few minutes of copulation the male moves backward and pulls the genital organs apart.

At the end of and after a copulation the female often walks forward, but she does not perform any restless behaviour. Disturb-

ance of the female during the intermediate amplexus may release attempts to establish copulation in the male (cf. Döhning). When a number of copulations have occurred the female may start to run. The male then starts to stimulate her, moving his antennae. But males have also been observed to leave a calm female after a number of copulations.

3. Subfamily S p o n d y l i n a e.

a. *Spondylis buprestoides* F.

The behaviour of this species is rather complex. The movements of the male antennae are very variable, consisting of type b, c, d, f, and g, components. The two antennae often move rather independent of each other. In most cases the fast but weak licking action (carried out upon the female's back during amplexus) and the sporadic licking (performed in the air some millimetres above the female's body during copula) are carried out with the maxillary palps alone. Since the female is normally quiet, it is uncertain whether the licking action has a signal value. However, when a female was disturbed as her legs were fastened experimentally with the fingers, the male stimulated her very actively performing scraping and biting actions.

During the first part of copula the male performs slow rhythmical penis movements, which push the ovipositor into the female abdomen and pull it out again. At a later phase of copula these movements of the ovipositor are performed by the female herself. During copula weak, horizontal tapping movements may occur. But no synchronization has been observed between the tapping, licking, or the penis movements. After some minutes of copula the male moves backward, and the genital organs separate. The female then begins to walk and the animals separate without any attempts by the male to resume the mating.

4. Family C h r y s o m e l i d a e.

a. *Donacia aquatica* L., subfamily Donaciinae.

Some parts of the behaviour of this species are similar to the behaviour observed in two other species of Donaciinae (see Michelsen, 1963). The antennal movements (type a) often hit the antennae of the female. During mating the male performs a 'wiping' action with his foremost tarsi, i.e. the tarsi placed upon the head or pronotum of the female move rhythmically. The

wiping action may move the female antenna or it may be performed upon the eyes of the female. Though a licking action is observed during amplexus and at the end of copula, it is rather weak and often performed in the air some millimetres above the female body. The pendulum movements are described on p. 333.

b. *Lilioceris lili* Scop., subfamily Criocerinae.

The behaviour of this species is very similar to that of most Lepturinae. The weak antennal movements performed during amplexus, beginning of copula, and at the end of mating, are of type g. In some cases the male produces sounds while being kicked by the female at the end of mating.

Phylogeny of the longhorned beetles.

Comparative ethology provides descriptions of the behaviour patterns of the present day species, and in several cases valuable information has been obtained on the phylogeny of the group by arranging the behaviour patterns according to variations and similarities. However, the model for the evolution of the tactile stimulatory actions presented elsewhere (Michelsen, 1966) implies that a convergent evolution may have been a regular feature during the evolution of the stimulatory behaviour in longhorned beetles. A comparative analysis of the stimulatory behaviour is therefore unlikely to contribute to the understanding of the phylogeny. Therefore, the comparison of the behaviour patterns presented below is based upon other parts of the sexual behaviour.

1. L e p t u r i n a e.

In a previous paper (Michelsen, 1963) the behaviour patterns of a few species were discussed with reference to 'normal' lepturine behaviour, this concept being identical with an 'average' behaviour including only actions found in all species. Since by investigation of a larger number of species the concept 'normal' cannot be upheld, the author has chosen the behaviour of *Gaurotes virginea* L. as the basis for comparisons. The behaviour of this species is rather simple, but the author does not intend to postulate that it should be near to the 'original' one.

The grouping of the behaviour patterns within the subfamily Lepturinae is indicated in fig. 9 which also includes a few species of the family Chrysomelidae. The figure is based upon the following considerations:

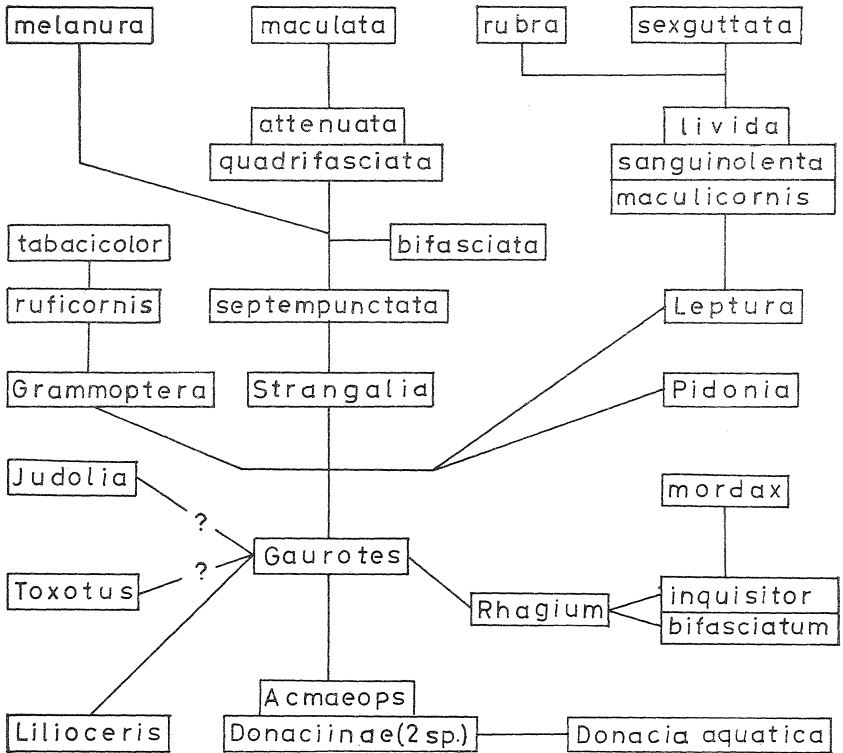


Fig. 9. The grouping of the behaviour patterns within the *Lepturinae*.

The genus *Rhagium* may be characterized by the presence of the round dance (Michelsen, 1963), which ends all matings in *R. inquisitor* and which has also been observed in *R. mordax* and *R. bifasciatum*. *R. mordax* seems to have lost the action of antennal movements, and pulling of the ovipositor occurs both in amplexus and at the end of copula, whereas this is not the case in *R. inquisitor* and *R. bifasciatum*. Though the males of *R. mordax* may bend their hindlegs around the female abdomen (cf. *Gaurotes*), the behaviour of *R. mordax* differs more from that of *Gaurotes* than does the behaviour of *R. bifasciatum* and *R. inquisitor*.

In the antennal movements during mating in *Pidonia lurida* and three *Leptura* species (*maculicornis*, *sanguinolenta*, and *livida*) the antennae bend between the first and second segments, the first segment staying immobile or moving less than the rest of the

antennae. Except for *L. livida*, these species show an amplexus behaviour like that observed in *Gaurotes*, i.e. during amplexus the males bend their hindlegs around the female abdomen and no pulling of the ovipositor is seen. During amplexus the males of *L. livida*, *sexguttata*, and *rubra* however, normally stretch their hindlegs and pull out the ovipositor, with the female raising her abdomen. During copula a pulling of the ovipositor has been observed in *L. quadrifasciata* (though the males of this species do not pull out the ovipositor at the establishment of copula). In *L. rubra* and *sexguttata* sounds are often produced in connection with matings (see p. 335) and the antennal movements in these species differ more from those of *Gaurotes* than do the antennal movements in the other species.

Though considerable differences have been found between the more 'advanced' behaviour patterns within the genera *Leptura* and *Strangalia*, the general behaviour patterns of the two genera are rather similar, e.g. males of *Strangalia septempunctata* may bend their antennae between the first and second segments. A comparison between four species of *Strangalia* has been attempted earlier (Michelsen, 1963). A gradual change in behaviour from *S. melanura* via *S. attenuata* and *S. quadrifasciata* to the strange behaviour of *S. maculata* was demonstrated. The behaviour of *S. septempunctata* and that of *S. bifasciata*—in spite of its remarkable copulatory behaviour (p. 336)—is closer to the behaviour of *Gaurotes* than is the behaviour of *S. melanura*, which was earlier considered a 'normal' strangalian behaviour.

While the behaviour of *Grammoptera tabacicolor* resembles that of a 'typical' *Leptura-Strangalia* (except for the peculiar position of the male upon the female), the behaviour of *G. ruficornis* is rather different (see p. 342).

The strange stimulatory behaviour of *Toxotus meridianus* (an arrhythmic pulling of the ovipositor) and *Judolia cerambyciformis* (biting of a female antenna) is probably the result of a complicated evolution (see Michelsen, 1966 and the comparison of the four *Strangalia* species, respectively). But since no other species in these genera have been examined, their positions are obscure.

The remarkable similarity between the behaviour of two species of the subfamily Donaciinae, Chrysomelidae (*Donacia semicuprea*

and *Plateumaris sericea*) and that of *Acmaeops collaris* L.*) has been described previously (Michelsen, 1963). In the behaviour of *Donacia aquatica* (p. 348) however, actions are found which have not yet been observed in cerambycid behaviour. On the other hand the behaviour of *Liliocerus lili* (subfamily Criocerinae, Chrysomelidae) is very similar to that of most lepturines (see p. 349).

2. S p o n d y l i n a e.

The behaviour of the *Spondylis buprestoides* male (p. 348) seems to be influenced by the inactivity of the female. The remarkable licking action thus seems to have a reduced signal value. On the other hand, scraping and biting actions may be released in the male by an artificially disturbed female. This, together with the complex antennal movements and the lack of synchronization between the individual actions, might suggest that the behaviour of *Spondylis* represents a secondary reduction due to the inactivity of the female from a rather 'advanced' type of behaviour.

3. C e r a m b y c i n a e.

The sexual behaviour within the subfamily Cerambycinae also shows some variations. However, the number of species studied does not allow any comparisons with reference to the phylogeny of the behaviour patterns at present.

Generally, the sexual behaviour demonstrated in most species within this subfamily is much more complex and/or 'extreme' than that of the 'typical' lepturine. This might indicate that the behaviour of the cerambycines represents an evolutionary more advanced level than that of the lepturines. Further, the fighting behaviour, which is almost lacking in the lepturines, has reached a rather advanced level in some cerambycines.

4. P h y l o g e n y o f c e r a m b y c i d e s.

Among the studies of the phylogeny of longhorned beetles, the contributions of Gahan (1911), Heintze (1925), Saalas (1936), Crowson (1953), and Linsley (1961) are the most important. Their results will not be discussed here but reference will be made to

*) The species *collaris* L., which has previously been called *Pachyta* (Redtb.) *collaris* L., should be referred to here as *Acmaeops* (Lec.) *collaris* L., since the name *Pachyta* (Zett.) is now used for another genus.

the family-tree constructed by Saalas (1936) on the basis of wing-venation. Concerning this diagram Crowson (1960) writes: 'The surprising thing about this diagram is that, for all the unsoundness of its ostensible basis, it does suggest the main outlines of cerambycid evolution'.

The main features of the phylogenetic diagram of Saalas are that Cerambycinae are thought to have evolved from lepturine ancestors, and that Spondyliinae (which are often regarded as a primitive group, cf. Heintze) are placed above Lepturinae. Both these postulates agree well with what has been suggested from the sexual behaviour.

As for the subfamily Lepturinae the diagram of the genera suggested by Saalas differs somewhat from that presented above. An examination of the figures in Saalas' paper however, suggests that a considerable part of the reduction in wing-venation might have occurred independently in the different genera. The diagram of Heintze, who based his conclusions mainly upon the morphological adaptations associated with the different types of feeding biology found in this subfamily, is more in accordance with that presented above.

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Summary.

The sexual behaviour of 19 species of longhorned beetles (Cerambycidae) and that of two species of Chrysomelidae are described. Some new stimulatory actions (scraping, biting, striking, and wiping) and

other actions (pendulum movements) have been found. Seven types of antennal movements have been found in the males. The fighting behaviour of 5 species has been studied. Observations have been made on the factors releasing some of the actions and on the production of sounds during sexual activity.

A model presented elsewhere (Michelsen, 1966) implies that a convergent evolution may have been a regular feature of the evolution of the tactile stimulatory actions. In this paper a comparative analysis is attempted for other parts of the sexual behaviour, and the results are discussed with reference to current theories on the phylogeny of the Cerambycidae.

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