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Notes on the Viviparous Cockroach *Gyna lurida* Saussure, 1855 (Blattodea, Blaberidae, Gyninae) especially on Courtship and Mating

Anmerkungen zur viviparen Schabe *Gyna lurida* Saussure, 1855 (Blattodea, Blaberidae, Gyninae), insbesondere zur Balz und Paarung

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Summary: We report on some morphological characteristics as well as on the reproductive behaviour of the viviparous, flying cockroach *Gyna lurida*. Females are larger than males and differ significantly in various body proportions (including body length and width, and length and width of the pronotum, both with and without tegmina). The relationships between pronotum width and body length as well as body width are largely linear in both sexes. The antennae of males and females do not differ in the number and types of sensory bristles and differ only insignificantly in the size of their annuli. The number of annuli is variable in both sexes. The courtship display of *G. lurida,* which has not been described in detail so far, is the most common type I known from the literature, in which the male finally raises its wings and the female then climbs onto the male's back to take up secretions from the tergal glands. During courtship, the males of *G. lurida* use their wings very frequently and intensively, beating them extremely quickly several times in succession, initially interrupted by short pauses. A receptive female then straightens up a little, turns to the then continuously fluttering male, rises, remains very briefly (maximum about 1 s) on his back with the head near the first abdominal tergites, while the male continues to flap his wings and then quickly descends with a turn of the body and assumes the usual mating position (abdominal end to abdominal end). Occasionally the male does not wait for a reaction from the female, but thrusts himself under the female, while flapping his wings. The first abdominal tergite of the male has a glandular field, which is covered by a loosely resting "cuticular membrane" (a protrusion of the articular membrane that connects metathorax and first abdominal tergite). Because of this and because of the extremely short time the female spends on the male, we assume that mainly volatile substances (pheromones) are released here, which are distributed with the rapid wing beats. In one female observed during oviposition, the time from the appearance of the ootheca to its complete disappearance in the brood sac was 1 h 45 min. The number of newborns varied between 9 and 27.

Key words: Sex dimorphism, reproduction, mating types, tergal glands

Zusammenfassung: Wir berichten über einige morphologische Merkmale sowie über das Fortpflanzungsverhalten der viviparen, flugfähigen Schabe *Gyna lurida.* Die Weibchen sind größer als die Männchen und unterscheiden sich signifikant in verschiedenen Körperproportionen (u.a. in der Körperlänge und -breite sowie in der Länge und Breite des Pronotums, jeweils mit und ohne Tegmina). Die Beziehungen zwischen Pronotumbreite und Körperlänge sowie Körperbreite sind bei beiden Geschlechtern weitgehend linear. Die Antennen von Männchen und Weibchen unterscheiden sich weder in der Anzahl noch in den Typen von Sinnesborsten und nur unwesentlich in der Größe der Annuli. Die Anzahl der Annuli ist bei beiden Geschlechter variabel. Die bisher nicht näher beschriebene Balz von *G. lurida* ist dem aus der Literatur bekannten häufigsten Typ I zuzuordnen, bei dem das Männchen letztendlich seine Flügel hochstellt und das Weibchen daraufhin auf den Rücken des Männchens klettert, um dort Sekrete aus den Tergaldrüsen aufzunehmen. Die Männchen von von

G. lurida gebrauchen während der Balz sehr häufig und intensiv ihre Flügel, mit denen sie, anfangs von kurzen Pausen unterbrochen, extrem schnell mehrmals hintereinander schlagen. Ein rezeptives Weibchen richtet sich daraufhin ein wenig auf, wendet sich zu dem dann ununterbrochen flatternden Männchen, steigt auf, verharrt ganz kurz (maximal etwa 1 s) auf dessen Rücken mit dem Kopf in Nähe der ersten Abdominaltergite, wobei das Männchen weiter mit den Flügeln schlägt, steigt dann rasch mit einer Drehung des Körpers ab und nimmt die übliche Paarungsstellung (Abdomenende zu Abdomenende) ein. Bisweilen wartet das Männchen nicht auf eine Reaktion des Weibchens, sondern drängt sich heftig mit den Flügeln schlagend und dabei evtl. rückwärts laufend unter das Weibchen. Das erste Abdominaltergit der Männchen besitzt ein Drüsenfeld, das von einer locker aufliegenden „cuticulären Membran" (eine Ausstülpung der Gelenkmembran, die den Metathorax mit dem ersten Abdominaltergit verbindet) bedeckt ist. Deswegen und wegen der extrem kurzen Zeit, die sich das Weibchen auf dem Männchen aufhält, vermuten wir, dass hier vor allem volatile Substanzen (Pheromone) abgegeben werden, die durch die raschen Flügelschläge verteilt werden. Bei einem während der Oviposition beobachteten Weibchen betrug die Zeit vom Erscheinen der Oothek bis zu ihrem vollständigen Verschwinden in der Bruttasche 1 h 45 min. Die Anzahl der Neugeborenen schwankte zwischen 9 und 27.

Schlüsselwörter: Geschlechtsdimorphismus, Paarungstypen, Balz- und Paarungsverhalten, Tergaldrüsen

1. Introduction

The cockroach genus *Gyna* Brunner von Wattenwyl, 1865, with currently more than 30 valid species, is mainly distributed in forested regions of tropical Africa (Beccaloni 2014; van der Wart 2015). The animals live in the floor of burrows, e.g. in termite nest cavities and in the mounds of driver ant nests. Relatively little is known about their biology in the natural habitat (Grandcolas 1993, 1994, 1997; Grandcolas & Deleporte 1998; Gautier 1980). Gautier (1980) has apparently also observed mating and mating attempts in the cave-dwelling *Gyna maculipennis*, but does not provide details. A species frequently kept in human care is the porcelain cockroach *Gyna lurida* Saussure 1899 from the forests of East Africa (Tanzania and Kenya) (www.cockroach.speciesfile.org; wirbellosenzentrum.de). It is a winged species up to about 3 cm long, with mostly whitish cream to dull brown upper wings (Fig. 1 A); meanwhile pure yellow strains are also known. The pronotum of the adults shows an apparently individual-specific pattern (Fig. 1 B-D). The nymphs are strikingly dark (brown to black)-white patterned (Fig. 1 F).

Despite their relative abundance, neither the primary nor the secondary literature provides more detailed information on the (reproductive) biology of *Gyna* species (see above). In a recent study on the "Phylogeny and life history of Blaberoidea (Blattodea)", in which molecular data are also used to investigate potential correlations between life history traits, Djernæs et al. (2020) only cite two articles on the Gyninae with some information on the number of offspring and the ootheca (see Grandcolas 1994; Grandcolas & Deleporte 1998), noting, however, that their mating type is not yet known. Generally, they define the reproductive mode as "ovoviviparity; ootheca carried internally until hatch" (p. 36). However, the term "ovoviviparity" implies from the outset that the young are not "signficantly" fed by the mother during pregnancy. We think that it may make more sense to call "ovoviviparous" cockroaches as viviparous and to expand the term "viviparity" only after an actual proof of food transfer from mother to offspring by the additions "lecithotrophic" and "matrotrophic" (Greven 1995; see also Greven & Zwanzig 2013; Greven et al. 2014, 2019). With the present observations on sexual dimorphism, remarkable courtship, duration

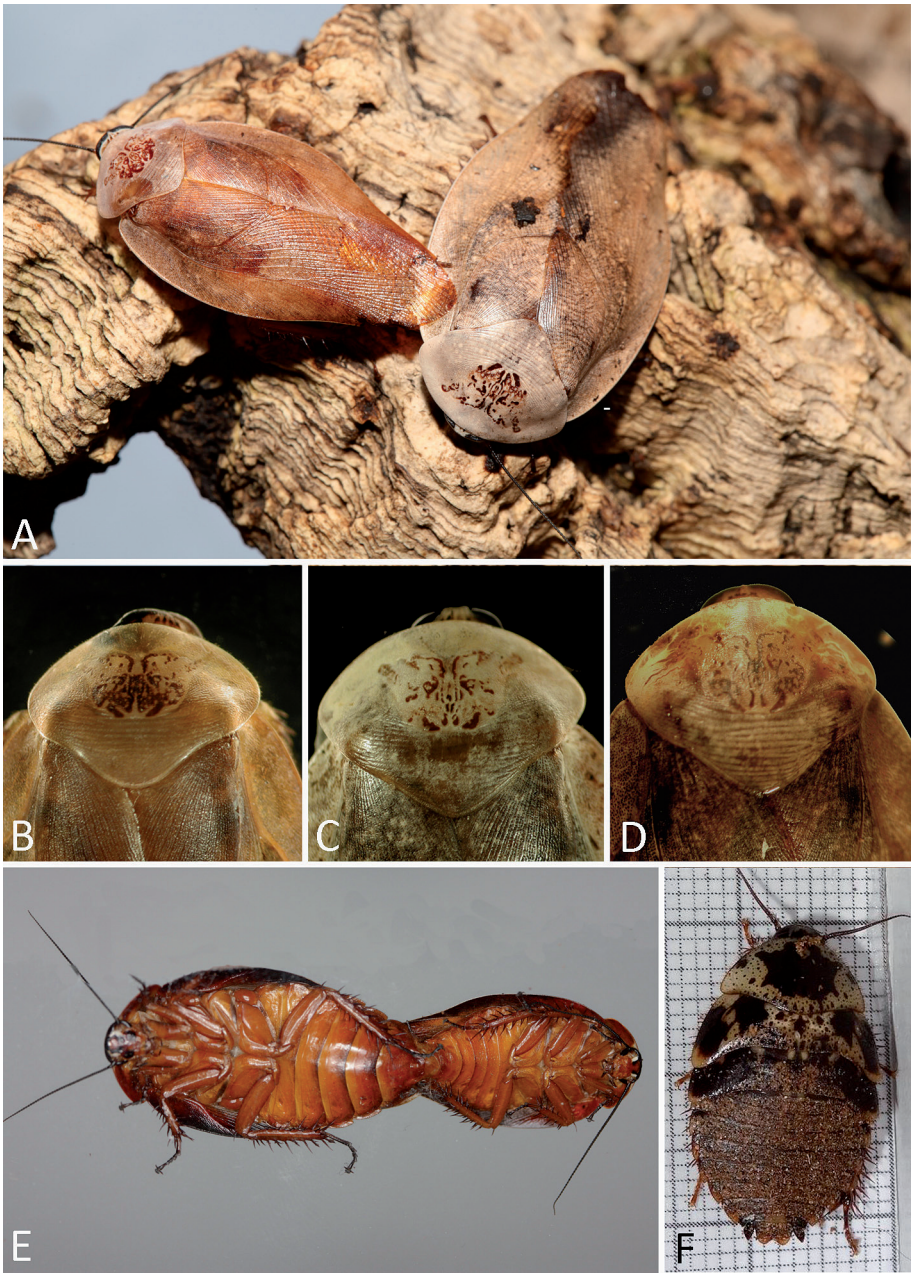


Fig. 1: Habitus and coloration of *Gyna lurida*. **A** Male (on the left) and female (on the right). Photo: W. Schulten. **B-D** Variability of the drawing pattern on the pronotum. **E** Mating. **F** Nymph with camouflaging substrate particles on the abdomen. Photo: J. Endres.

Abb. 1: Habitus und Färbung von *Gyna lurida*. **A** Männchen (links) und Weibchen (rechts). Foto: W. Schulten. **B-D** Verschiedene Zeichnungsmuster des Pronotums. **E** Paarung. **F** Nymphe mit tarnenden Substratpartikeln am Hinterleib. Foto: J. Endres.

of gestation and number of neonates, we extend the information on the reproductive biology of *G. lurida* and complement our previous studies on viviparous cockroaches (see citations above).

2. Material and methods

2.1. Origin and keeping of the cockroaches

The breeding stock of *Gyna lurida* Saussure, 1899 (Blaberidae, Blattodea) came from the pet trade. The cockroaches were kept in a top-ventilated (wire gauze) plastic box (55 x 33 x 33 cm). The bottom was covered with a layer of regularly moistened coconut substrate about 9 cm high and empty egg cartons and rolls of kitchen paper. Above the box were two heat lamps that alternately illuminated the container (60 Watt Exo Terra terrarium heat lamp from 09:00 to 21:00; 40 Watt Zoo Med lightless ceramic bulb from 21.00 to 9:00). The temperature varied between 25 °C (at night) and 32 °C (during the day). Smaller groups of cockroaches or individual animals were kept in plastic containers of different sizes with largely identical light and temperature conditions The animals were fed with fruit and vegetables (mostly carrots, potatoes, peppers, lettuce, apples or bananas), occasionally also with leftovers (e.g. meat).

2.2. Morphology

Phallomere sclerites: The phallomer sclerites in the sixth and seventh segment of three males were removed, freed from the adhering tissue with 10% KOH, rinsed in water and mounted on slides with polyvinyllactophenol..

Sex dimorphism: Measurements (maximum pronotum width, pronotum length along the median line, body length up to the posterior tip of abdomen excluding cerci with wings and ventral body length and greatest width of the body without wings were made on photos (on graph paper, taken with a Sony Digital Camera HX50) of the dorsal and ventral side of ten males and ten females using the freeware programme "CAD-KAS Bildvermessen. Significances were determined using the Man-Whitney-U-Test (alpha = 0.05).

Antennae: The antennae of five females and five males were cut off below the scapus and enclosed on slides in polyvinyllactophenol. Using photos and the programme "Snake Measure Tool" we measured their total length including the pedicellus and counted the total number of annuli. In addition, the length and width (near the distal rim of bristles) of selected annuli were determined centrally from joint to joint. The antennae of an ethanol-fixed female was air-dried, sputtered with gold and examined using a scanning electron microscope (SEM Leo 1430, Fa. Zeiss).

Tergal glands: The adominal tergites including parts of the metathorax of several males and females (ethanol-preserved) were dissected along the pleural membrane, freed from the underlying tissue with 10% KOH, rinsed in water and mounted in polyvinyllactophenol (see above) or the metathorax plus the first abdominal tergits were dehydrated with ethanol, air-dried, sputtered with gold and examined in the SEM (see above).

2.3. Behavioural observations

2.3.1. Courtship and mating

In preliminary experiments, conditions (lighting, time of day, temperature, virgin still white females immediately after imaginal moult and later after the sclerotization of the cuticle) for mating readiness were checked in different containers. Finally, four females (before and after sclerotization) as well as another four already sklerotized virgin females were videographed at temperatures

> 20 °C at different times of day (between 8:00 and 2:00) under different lighting conditions (natural light, dimmed light, red light) in a simple "mating-behaviour observation box". This box consisted of a cardboard box (W 16 x D 19 x H 23.5 cm), which was only open at the front so that the cockroaches could also stay on the ceiling. The box was trimmed so that the bottom surface overlapped the ceiling surface, so that an animal falling from the ceiling could not fall out of the box. In case of matings on the ceiling of the box, a 12 x 15 cm mirror was placed on the floor so that nearly the whole area usable by the animals could be viewed with the camera (Fig. 2). Here, six complete courtship and mating sequences and 45 courtship sequences (without subsequent mating) were observed and partly videographed.

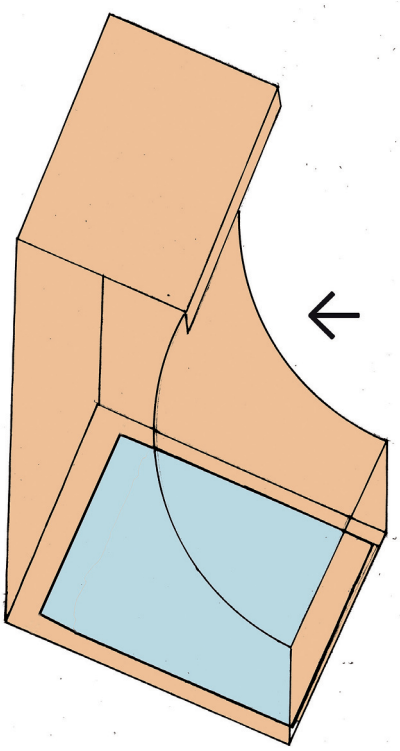


Fig. 2: Observation box with open side (arrow; for further explanations s see text). Mirror (blue).
Abb. 2: Beobachtungsbox mit offener Seite (Pfeil; weitere Erklärungen s. Text). Spiegel (blau).

2.4. Oviposition, gestation period and births

The six successfully mated females were housed individually in small containers with some soil substrate. If known, the time of oviposition was noted. The same procedure was followed with three females, whose oviposition could be observed in the mass breeding. The substrate was sieved at least every two days and searched for newborns.

2.5. Documentation

For the photo documentation, a "Canon EOS 500D Digital SLR" SLR camera (macro lens "EF-S 60 mm f/2.8 MACRO USM" and ring flash "MR-14EX") was used. Video recordings were made using a digital camera (DMC-TZ81, Lumix Panasonic). Microscopic recordings were made on the Olympus Vanox TAH-2 microscope or a dissecting microscope (Olympus SZH) with the C-3030-Z digital camera. The video recordings were edited and processed on the computer using the programms "Gimp 2" and „DaVinci Resolve".

3. Results

3.1. Structure of the phallomeres

The phallomeres consist of three sclerites from the last two segments. The first sclerite of the left phallomere "L1"has two lobes, of which the lower lobe is well supplied with setae, wheras the upper lobe is glabrous. The second sclerite of the left phallomere "L2" consists of the dorsal hook-shaped sclerite L2d and the ventromedian sclerite L2vm. The hook-shaped L2d is a relatively flat plate which emerges from the preputial membrane as a sclerotised part. It is not connected to the elongated L2vm. Its outline conforms to the shape of the prepuce. The hooked sclerite of the right phallomere R2 has a subapical incision (Fig. 3).

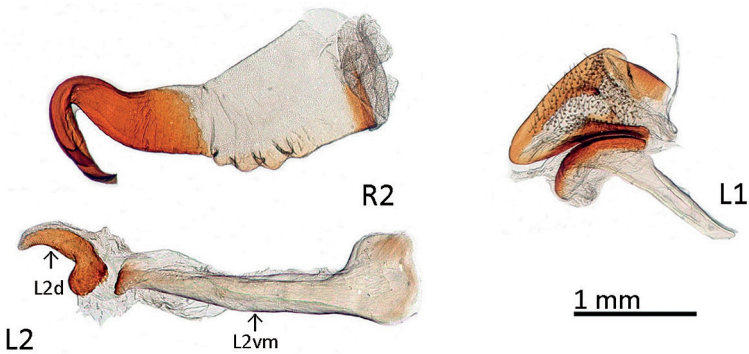


Fig. 3: Sclerites of the male genital apparatus of *Gyna lurida*. Hooked sclerite of the right phallomere (R2). The second sclerite of the left phallomere (L2) consisting of L2vm (ventro-medial) and L2d (dorsal);. The first sclerite of the left phallomere (L1).
Abb. 3: Sklerite des männlichen Genitalapparates von *Gyna lurida*. Hakenförmige Sklerit des rechten Phallomers (R2). Das zweite Sklerit des linken Phallomers (L2) aus L2vm (ventro-medial) und L2d (dorsal). Erstes Sklerit des linken Phallomers (L1).

3.2. Morphometric data

The males are significantly smaller than the females. This is true for all masses taken: Length with Tegmina (males 25.9 ± 3.53 mm; females 32.05 ± 3.53 mm; p = 0.0059). Width with tegmina (male 13.2 ± 1.8 mm; female 16.2 ± 1.8 mm; p = 0.0089). Length without wings (male 22.2 ± 2.6 mm; female 26.9 ± 2.6 mm; p = 0.0055). Width without wings (male 9.8 5 ± 1.87 mm; female 13.3 ± 1.87 mm; p = 0.0057). Length of pronotum (male 6.4 mm ± 0.85 mm; female 7.53 ± 0.85 mm; p = 0.0166). Width of pronotum (males 8.6 ± 1.45 mm; females 11.2 ± 1.45 mm; p = 0.0056).
The various relationships of the measured parameters such as prontum length, pronotum width , body length and body width with and without tegmina are more or less linear and also confirm the significant size differences between females and males (Fig. 4) . Only in the relationship between lenght of the pronotum and width of the body (Fig. 4 E) and lenght of he pronotum and the body with tegmina (Fig. 4 F) the clear separation blurred.

3.3. Antennae

The antennae consist of the scapus, which articulates directly on the head, the pedicellus and the annuli, the first of which is the primary growth zone (meristem) (Fig. 5 A-K). The length of the intact antennae of males averaged 13.4 ± 0.2 mm (n = 3), that of females 13 ± 0.35 .mm (n = 4). The number of annuli of both antennae was variable in both sexes. The highest number (without the scapus) was 65, the lowest 55 (in one male). In the latter, two annuli were fused
The flagellum can be roughly divided into three sections based on the distribution pattern of the sensory bristles (Fig. 5 C-K). Characteristic for the most annuli is a ring of strong and long sensilla near their distal ends. On older segments (middle and end section) more long and numerous small bristles appear. The annuli themselves have a scaly structure (Fig. 5 L). We did not see significant differences in the amount and the types of sensilla between the antennae of females and males.
Shape and size of pedicellus and first annulus are variable (different length, square,

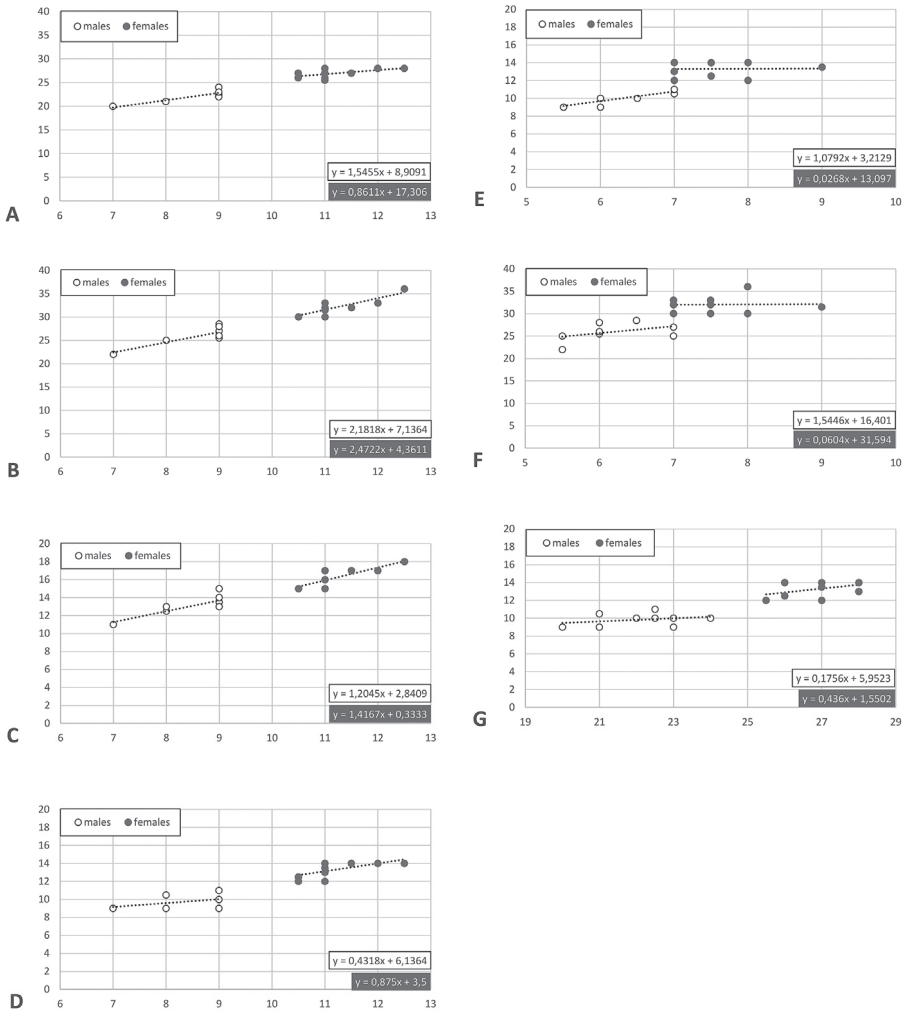
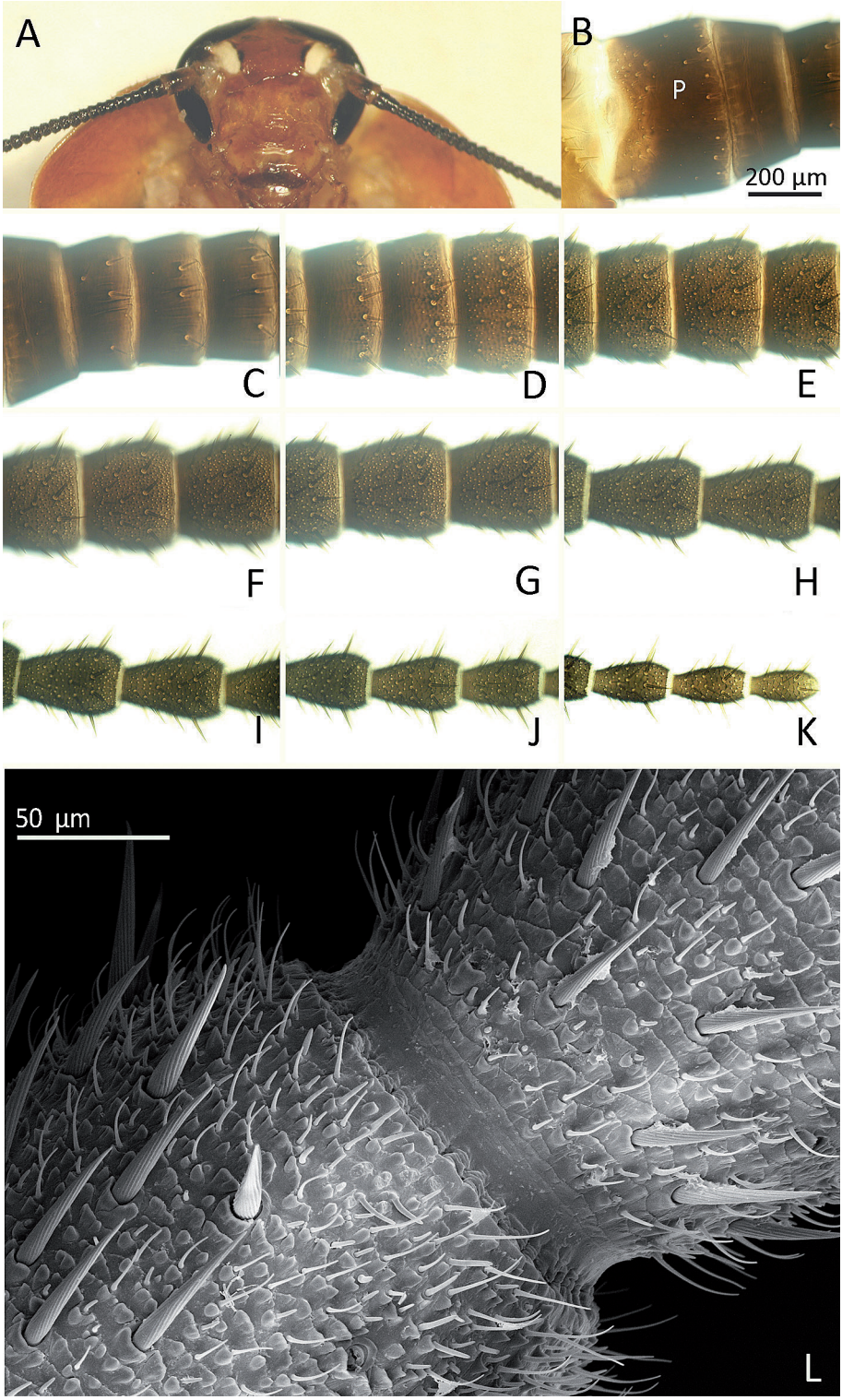


Fig. 4: Relationshps between pronotum width (abscissa A-D) of males and females to body length without (**A**) and with tegmina (**B**), to body width with (**C**) and without (**D**) tegmina, pronotum length (abscissa E, F) with (**E)** and withthout (**F**) tegmina, and body length (abscissa to body width (**G**). N =10; dots < than 10 are based on congruent measurements. Units of measurements in mm.

Abb. 4: Beziehungen zwischen Pronotumbreite von Männchen und Weibchen zu Körperlänge ohne (**A**) und mit Tegmina (**B**), zur Körperbreite mit (**C**) und ohne (**D**) Tegmina, der Pronotumlänge (Abszisse E, F) mit (**E**) und ohne (**F**) Tegmina sowie der Körperlänge (Abszisse) zur Körperbreite (**G**). (n = 10; Punktezahl < 10 beruhen auf deckungsgleichen Messungen. Maßeinheiten in mm.

trapezoid etc.), but the first segments (after the scapus) are clearly broader than long in all specimens, and they even seem to increase slightly in width up to about the 10th segment, but then become relatively longer and narrower in the apical direction, especially in the last third of the antenna (Fig. 5 B-K).


A
B
P
200 µm
C
D
E
F
G
H
I
J
K
50 µm
L

3.4. Tergal glands

In both sexes the first abdominal tergite is relatively large; it has a whitish field running longitudinally and apparently slightly raised, which is covered by a "cuticular membrane" (Fig. 6 A, B, E), which appears to be a a protrusion of the articular membrane that connects metathotax and first abdominal tergite. This „cuticular membrane" lies with its free edge loosely on the first adominal tergite. so that it can be lifted off (Fig. 6 G). Under the "membrane" there are glands on the witish field but only in males. These tergal gands are visible as variously shaped depressions, each with a different number of glandular orifices (Fig. 6 C, G, H). In a deeper level, the corresponding cuticular excretory ducts become visible (Fig. 6 D).

3.5. Courtship and mating

Occasionally (three times in experimental boxes and once in mass breeding), males could be observed in the presence of one or more females and other males fanning their wings and apparently rubbing their abdomina several times against the inner surfaces of the hind wings ("wing rubbing"). Between these actions, the male fluttered briefly before sometimes repeating the action. He then began to wander around, briefly flapping its wings from time to time (Fig. 7).

The courtship always began with the male scanning a female with his antennae (Fig. 8 A). He occasionally climbed on the female, but usually walked sideways along the female, often circling her, with his head clearly tilted towards the female. During this phase it could happen that the male lost interest or that the female simply moved away. If neither was the case, the male stopped diagonally in front of the female's head and then turned his abdomen towards her. From this point on, two slightly different "strategies" of the males were evident.

"Strategy 1": The male began to flap his wings several times with high frequency in short phases (approx. 0.5 s) at intervals of about 1.5 s (Fig. 8 B-E). The female either fled or reacted (but not always) to this behaviour – in some cases already after the first fluttering phase – by turning slightly erect and jerking towards the diagonally standing male and pausing briefly. In most cases, however, the male had to repeat these fluttering phases many times to attract the female's attention. In one case, where the female was not interested, the male fluttered 37 times in a row (with sometimes much longer pauses between the individual flutter phases) until he touched the female again and then gave up. However, if the female turned to the male, the male responded by continuing to flap his wings (Fig. 8 F, G) until the final mating position was reached (see below). When the female was ready to mate after remaining in the upright position, she climbed very quickly onto the male's back and remained there very briefly (for a maximum of 1 s, but usually shorter) with her head close to the anterior tergites, while the male continued to flutter with his wings raised and sideways spread (Fig. 8 G, H). Typical "feeding movements" of the female could not be identified because of

Fig. 5: Annuli of the antenna. **A** Head of a a male with antennae. **B** Scapus (left) and Pedicellus (P). **B-K** Representative annuli from base to tip. Note the different density and distribution of sensory bristles. **L** Two annuli from the middle region of an antenna with large and small sensory bristles and scaly surface (SEM image).

Abb. 5: Annuli der Antenne. **A** Kopf eines Männchens mit Antennenansatz. **B** Scapus (links) und Pedicellus (P). **B-K** Repräsentative Annuli von der Basis bis zur Spitze. Man beachte die unterschiedlichen Dichte und Verteilung der Sinnesborsten. **L** Zwei Annuli aus der mittleren Region einer Antenne mit großen und kleinen Sinnesborsten und schuppiger Oberfläche (REM-Aufnahme).

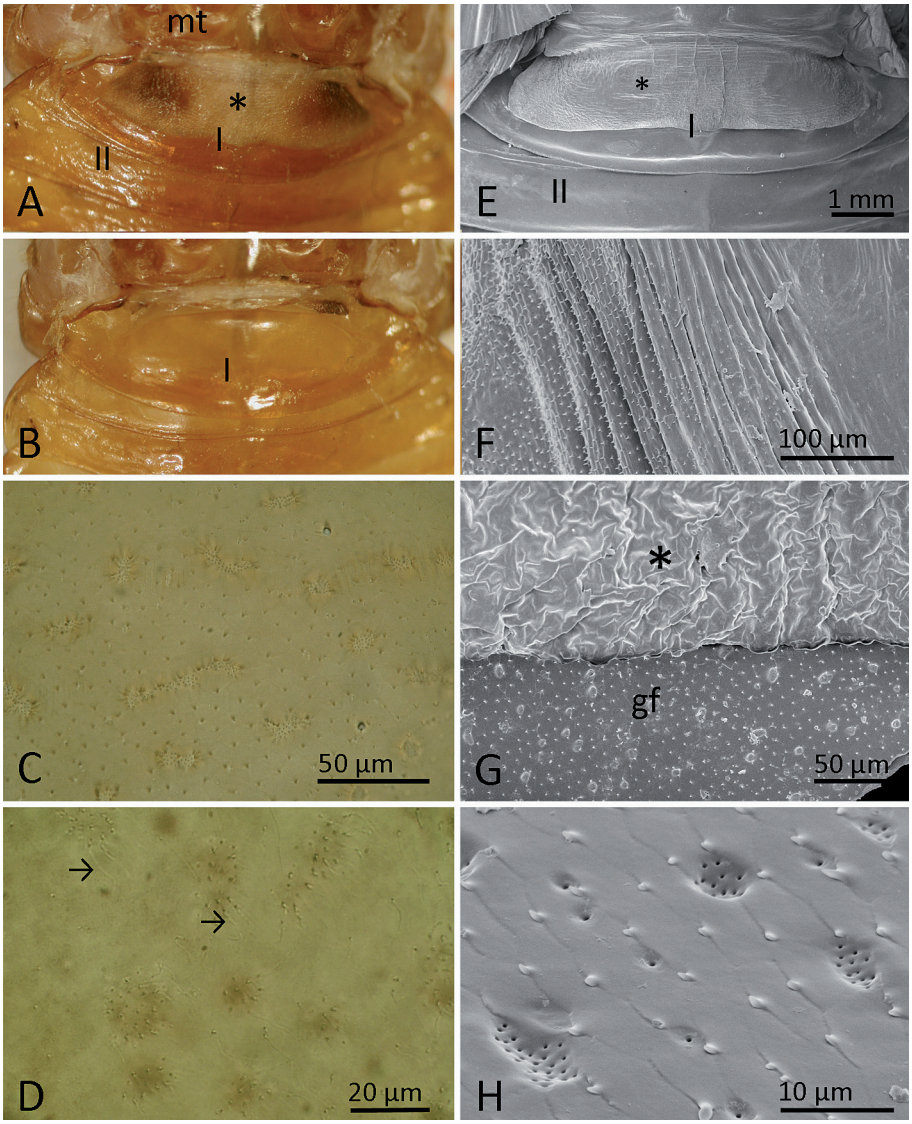


Fig. 6: Metathorax (mt) and abdominal tergites (I, II) of a male. **A** First tergite (I) with overlying "cuticular membrane" (asterisk). **B** Ditto, but without this "membrane". **C** Glandular field with numerous irregularly distributed depressions on the 1st tergite. **D** Glandular excretory ducts (arrows) in a deeper plane. **E** First tergite (I) with overlying "membrane" (asterisk). **F** Articular membrane at the transition of the "cuticular membrane" to the metathorax (right). **G** Glandular field (gf); above the partially removed "membrane" (asterisk). **H** Detail of the depressions with several but also individual glandular openings. E-H SEM images.
Abb. 6: Metathorax (mt) und die Abdominaltergite (I, II) eines Männchens. **A** Erstes Tergit (I) mit aufliegender „cuticulärer Membran" (Stern). **B** Dito, aber ohne diese „Membran". **C** Drüsenfeld mit zahlreichen unregelmäßig verteilten Vertiefungen auf dem 1. Tergit. **D** Drüsenausführgänge (Pfeile) in einer tieferen Ebene. **E** Erstes Tergit (I) mit aufliegender „Membran" (Stern). **F** Gelenkmembran am Übergang der „cuticulären Membran" zum Metathorax (rechts). **G** Drüsenfeld (gf), darüber die zum Teil entfernte „Membran" (Stern). **H** Detail der Vertiefungen mit mehreren aber auch einzelnen Drüsenöffnungen. E-H REM-Bilder.

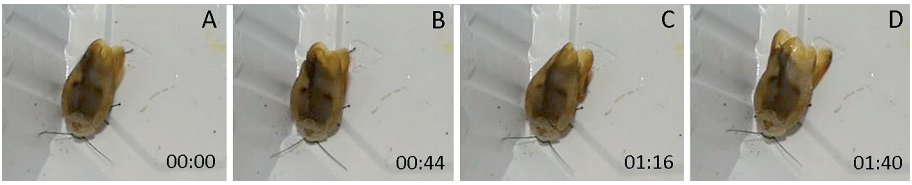


Abb. 7: Fanning out and rubbing the wings in a male. From a video sequence with indication of the time.
Abb. 7: Auffächern und Reiben der Flügel bei einem Männchen. Aus einer Videosequenz mit Zeitangaben.

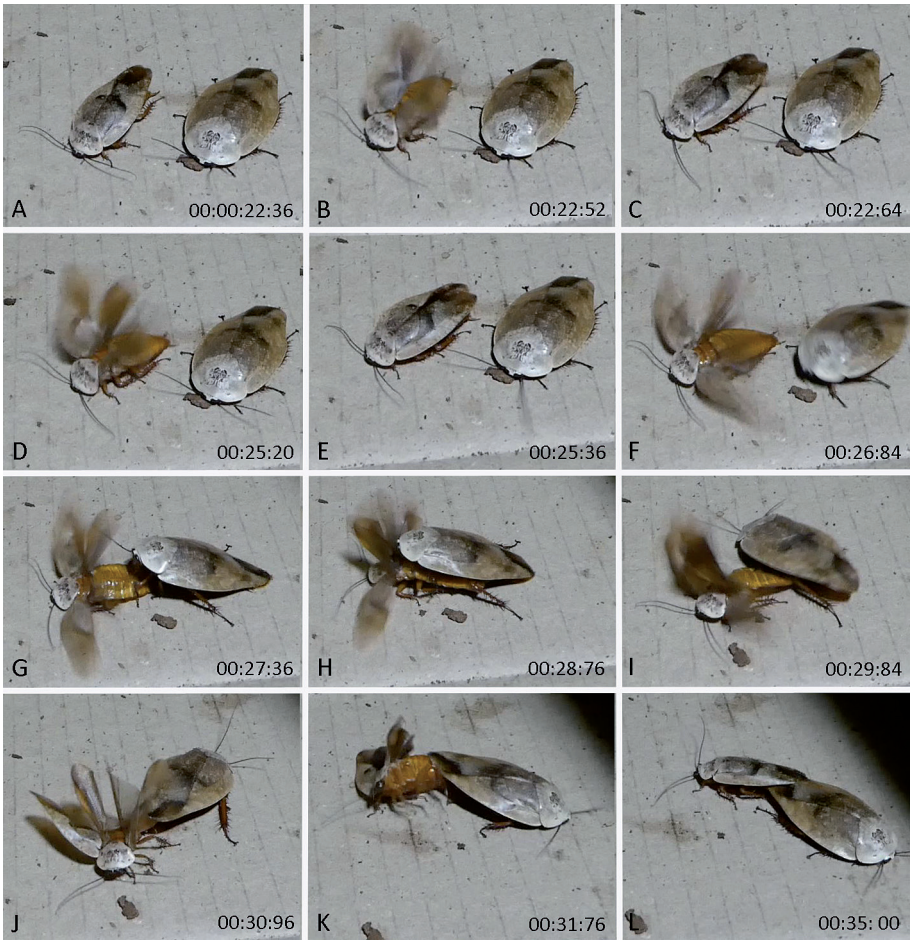


Fig. 8: Typical mating sequence ("strategy 1") of *Gyna lurida*. **A** The smaller male (left) gropes for the female with his antennae. **B-E** The male flaps his wings briefly, with short pauses in between. **F** The male flutters continuously, the female turns towards him. **G-K** The female climbs onto the male's back and immediately turns to make genital contact. **L** The pair reach the mating position and the male puts on his wings. From a video sequence with indication of the time.
Abb. 8: Typischer Paarungsablauf („Strategie 1") von *Gyna lurida*. **A** Das kleinere Männchen (links) tastet mit seinen Antennen nach dem Weibchen. **B-E** Das Männchen flattert kurz mit den Flügeln, dazwischen liegen kurze Pausen. **F** Das Männchen flattert ununterbrochen; das Weibchen wendet sich ihm zu. **G-K** Das Weibchen klettert auf den Rücken des Männchens und dreht sich unmittelbar danach, um den Genitalkontakt herzustellen. **L** Das Paar gelangt in die Paarungsposition; das Männchen legt die Flügel an. Aus einer Videosequenz mit Zeitangaben.

the shortness of the process. Afterwards, the female turned (at least) 180° on the male, while the genital contact was made (Fig. 8 I-L). From the start of continuous fluttering (when the female straightened up a little to signal interest to the male) to the final mating position, 3 to 4.5 seconds passed, depending on how quickly the female climbed onto the male and turned around on him. The turn occasionally took place further than 180° (once even about 270°), which also caused the then hooked male to be pulled a greater distance to the side e and dragged through the tank by the female. Only in the final opposite-linear position the male stopped flapping his wings. These wings were put on during the subsequent mating and overlapped the wings of the female. The now applied wings always overlapped the female's wings during the subsequent mating (Fig. L; see also Fig. 1 E).

If the female did not react, moved away or was not ready to mate after remaining in the described upright pose, the male stopped flapping his wings after a while, turned around and groped for the female (when still in vicinity). In some cases the male started courtship again.

"Strategy 2": The male did not wait for a reaction from the female, but pushed backwards running and fluttering from the side under the female, which either fled or turned to the male and climbed on his back.

In one case it was observed that a male, after meeting a still white virgin female, fluttered briefly nine times, but the female fled. In three cases, when courtship was relatively advanced – the female was already turning on the male – apparently no genital contact was made. In two cases, the males courted again and successfully came to mate. In another case, the pair remained sitting with abdominal contact in the usual mating position for about 4 min until the male broke this contact, turned around and groped for the female.

3.6. Oviposition, gestation and number of newborn

In a single female observed continuously during oviposition, the time from the appearance of the ootheca to its complete disappearance in the brood pouch was 1 h 45 min. Four pairs spent 35, 48, 51 and 72 min in mating position. The number of newborns at 5 births was 9, 11, 14 , 27 and 29. The time between mating and birth of the young was 50 and 62 days in two females; the time between oviposition and birth was 27 and 33 days in two other females.

4. Discussion

4.1. Sexual dimorphism

The organisation of the phallomers coincides with that described by ROTH (1972) for *Gyna lurida*. In addition, our measurements prove the most visible differences in the body length of males and females, also for other body proportions. Females being larger than males is not uncommon in cockroaches and applies to a relatively high percentage of species (e.g. BELL et al. 2007; DJERNÆS et al. 2020).

The antennae of *G. lurida* are "typical" cockroach antennae with scapus, pedicellus and flagellum (the latter with a relatively manageable number of annuli). Neither our measurements nor the light microscopic inspection revealed particular differences in the length of the antennae, their (varying) number of annuli (such a variation seems to be common in cockroaches, e.g. FUJITA & MACHIDA 2014) and in their equipment with sensory bristles (chemoreceptors and mechanoreceptors), which we, however, have not characterized in more detail. The width and length of the annuli seemed to be slightly smaller in females. However, as the individual values varied considerably and overlapped strongly and the sample size was also too small, definitive statements are not possible.

4.2. Conditions for successful observations

Compared to the total number of our experiments (including the mostly unsuccessful preliminary experiments not described in detail here), the yield of courtship sequences and completed matings was very low. However, some conditions for successful courtship and mating can be deduced from this.
1) As expected and according to the habitat of the animals (see above), the temperature plays an important role. Generally, *Gyna lurida* should be kept at temperatures > 20 °C (cf. also https://insektenliebe.com/). At temperatures < 20 °C the cockroaches did not mate.
2) Females immediately after the imaginal moult are neither receptive nor particularly attractive for males (only one short courtship occurred in front of such a female).
3) Even completely sclerotized virgin females are not always willing to mate, but may flee in early stages of courtship (fluttering of the male at short intervals). Only in one encounter the female had already climbed on the male, but dismounted immediately thereafter.
4) All observed courtship activities and possible subsequent matings took place at very different times of day and under different light conditions. Therefore, the time of day should not have any particular influence on the sexual activities of *G. lurida*. Only in very bright light neither courtship nor mating could be observed.
Our still very preliminary observations on activity (flying, running) show that the adults and nymphs of *G. lurida* spend a lot of time in the substrate (humus), that the adults, as with many other cockroaches, are mainly active in the early evening hours (cf. Bell et al. 2007) and that the larger females also fit to fly seem generally less active than the males. Furthermore, pregnancy is very likely to influence the activity of the females (cf. Meller & Greven 1996; Greven et al. 2014), but we do not yet know anything about this in *G. lurida*.

4.3. Mating behaviour

Cockroaches find their mates in different ways. Either the males or females attract the other sex from a greater distance via volatile pheromones, or the sexes find each other rather accidentally and corresponding pheromones only act at shorter distances (e.g. Sreng 1993; Gemeno & Schal 2004; Lizeé et al. 2017). How the mates of *Gyna lurida* find each other – whether from a greater distance or only when they are close –, and whether the attraction comes from the female or male is not (yet) entirely clear. Perhaps of significance here is that the males rub their abdomen against the fanned out underwings and briefly flap their wings. This was occasionally observed in mass breeding, but also in experiments in which several individuals (males and females) were in the observation box at the same time. However, a signalling effect on other males is just as likely.
After the mates have found each other, the male feels the female with his antennae. Thereafter, cockroaches use different "mating patterns" depending on the species (cf. Sreng 1993; summarised in Bell et al. 2007; see also Djernæs et al. 2020): (1) The male raises his wings and may also lower them again ("wing raising display"); the female climbs onto the male, apparently taking up secretions (aphrodisiacs) from the male's tergal glands ("feeding response"); subsequently, genital contact ("copulation") is established. This is apparently the most ancestral and widespread type. (2) The male mounts the receptive female and then makes genital contact (very rare), and (3) neither the male nor the female mounts, but the male positions himself behind the female with his head in the opposite direction, walks backwards and makes genital contact. Djenæs et al. (2020) are of the opinion that type 2 and

3 have evolved several times (predominantly in the Blaberidae) independently from type 1. Recently, another mating type has been described in *Oxyhaloa deusta*, in which females attract males via pheromones and males do not lift their wings but circle the female until she mounts the male (LIZEÉ et al. 2017; GREVEN et al. 2019). The phylogenetic evaluation of this mating type is apparently still largely pending (LIZEÉ et al. 2017). The terminal position – heads facing in opposite directions – is identical in all mating types (e.g. SRENG 1993; GEMENO & SCHAL 2004; BELL et al. 2007; LIZEÉ et al. 2017).

The courtship display of *G. lurida* is to be classified as type 1. However, the intensity (duration, frequency, speed) of the wing beating before mounting – the female offers herself after such actions (not always) by turning to the male and slightly standing up – and also during the short time the female is on the male's back is remarkable. The wings were not kept motionless at any time as in many other cockroaches that show mating pattern 1 (e.g. BARTH 1964; GREVEN & ZWANZIG 2013; cf. also BELL et al. 2017). Incidentally, the male can also mate without the clear consent of the female (which appears to be expressed by the straightening and the turning towards the male), by forcing himself under the female while flapping his wings violently ("strategy 2"). This almost looks as if the female is being forced to mate, but in the observed cases a successful mating still occurred.

The time the females spent on the male, who was still flapping his wings vigorously, was 1 s at the most. Even though the females of cockroaches generally stay on the male only for a relatively short time during courtship – the data in this respect are sparse; usually 2 to 7 s are given (cf. BARTH 1964; BELL et al. 2007), in some species even up to 1 min (BARTH 1968) – the time of 1 s in the case of *G. lurida* seems very short to us. During this short time, no typical "feeding movements" of the female could be observed.

Generally, chemical, visual, tactile and acoustic signals play a role in mate finding and courtship in cockroaches (GEMENO & SCHAL 2004). Riding on is certainly an advanced stage of courtship; the partners have already found each other via contact pheromones and/or volatile pheromones. In the case of *G. lurida*; the male presented his exposed dorsal surface to the female, at least intermittently, while vigorously flapping his wings to encourage her to mount and allow her to perceive glandular secretions. In general, these secretions come from tergal glands, which, depending on the taxon, may be associated with clearly visible cuticular modifications such as tufts, setae, ridges etc., but most Blaberidae lack them (ROTH 1969; SRENG 1993, 2006). Here, tergal glands open only via small groups of glandular orifices (e.g. SRENG 1993, 2006). Up to now, neither such specialised fields nor spectific tergal glands were known from *G. lurida* (s. ROTH 1969). However, we could show a male-specific field of tergal glands on the 1st abdominal tergite covered by a specific unusual "cuticular membrane" (this "membrane" is also present in females and apparently is a specific formation of the articular membrane). The glands open into depressions of the cuticle, as is also known from other Blaberidae (see SRENG 2006). The behaviour of the animals (extremely short inspection of the anterior abdominal tergites by the female accompanied by violent wing flapping of the male) as well as the fact that the glandular field is covered by a "cuticular membrane", rather suggest that predominantly volatile secretions are emitted, which may be spread by the violent wing beats. This would mean that the secretions here are perceived less via a contact chemorepetion, but rather via olfactory processes (see SRENG 1993). Already BARTH (1964, 1968) had suggested that vibrations and wing fluttering of some cockroach species during courtship could generate air currents that could serve to spread pheromones (see als FUJITA et al.

2020). Generally, behaviours that produce airborne or substrate-transmitted vibrations, such as different body movements of the male, including wing pumping and wing fluttering, and even vocalisations in some species (e.g. *Nauphoeta cinerea*), are discussed as components of cockroach courtship (summarised in Bell et al. 2007).

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