Entomologie heute 25 (2013): 77-97

Courtship, Mating, and Organisation of the Pronotum in the Glowspot Cockroach *Lucihormetica verrucosa* (Brunner von Wattenwyl, 1865) (Blattodea: Blaberidae)

Balz, Paarung und Organisation des Pronotums der „Leuchtschabe" *Lucihormetica verrucosa* (Brunner von Wattenwyl, 1865) (Blattodea: Blaberidae)

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Summary: *Lucihormetica verrucosa* is a viviparous cockroach with a remarkable sexual dimorphism; males possess two symmetrically arranged yellow spots on their pronotum considered as luminescent organs. After a relatively stereotyped courtship, mating takes place according the well-known type 1, i. e. the male offers himself the female, arises his wings, which remain elevated until the female climbs onto the males back; then he makes genital contact. In some trials, however, males completely climbed upon the female prior to that. When dismounting, the female turns round so that heads of mates show in the opposite direction and the male inserts his phallomer. Although males already court pale and teneral females immediately after the imaginal moult, females respond to courtship and became receptive not before the 20th day after the final moult. Histological sections and SEM-pictures do not support the opinion that the yellow spots are light organs. The cuticle covering the spots is translucent with the exocuticle considerably reduced. The surface of this cuticle is equipped with small knobs each bearing a small mechanoreceptor (?). In the area of the spots immediately below the epidermis a large pad of hypertrophied fat body cells is located with large tracheae running through it. These cells obviously accumulate carotenoid-containing lipid droplets. As the presence of the yellow spots is sex-specific, as their size that slightly differs on both sides (not ascertainable with conventional statistics) is positively correlated with the width of the pronotum, and as their shades depend on a carotenoid-containing diet, we think that these markings are condition-dependent traits that could play a part in mate choice and/or intraspecific aggression, but also could serve as warning signal.

Keywords: Courtship and mating, pronotum, asymmetry, condition-dependent character, carotenoids, fat body

Zusammenfassung: *Lucihormetica verrucosa* ist eine vivipare Schabe, deren Männchen zwei auffallende, symmetrisch angeordnete gelbe Flecken auf dem ansonsten relativ variabel gezeichneten Pronotum besitzen, die als Leuchtorgane gedeutet werden. Nach einer relativ stereotypen Balz paaren sich diese Schaben weitgehend nach dem aus der Literatur bekannten Typ 1, d. h. das Männchen bietet sich dem Weibchen an, indem es seine Flügel hebt, und wartet, bis das Weibchen aufsteigt; dann wird der Genitalkontakt hergestellt. In einigen Versuchen bestieg allerdings das Männchen vorher das Weibchen. Während des Absteigens dreht sich das Weibchen so, dass die Köpfe der Tiere in entgegengesetzte Richtung zeigen. Die Genitalregionen beider Partner bleiben verbunden und das Männchen führt sein Phallomer ein. Obwohl Männchen bereits noch fast weiße, sehr zarte Weibchen unmittelbar nach der Imaginalhäutung anbalzen, sind diese offenbar erst etwa ab dem 20. Tag nach der Imaginalhäutung rezeptiv und erwidern die Balz. Histologische und rasterelektronenmikroskopische Untersuchungen geben keine Hinweise darauf, dass die gelben Flecken Leuchtorgane sind. Die die gelben Flecken bedeckende Cuticula ist durchsichtig und ihre Exocuticula stark reduziert. Ihre Oberfläche besitzt kleine Erhebungen, die jeweils mit einem kurzen Sinnes„haar" (Mechanorezeptor?) besetzt sind. Unmittelbar unter der Epidermis liegt ein großes, von Tracheen durchzogenes Polster von hypertrophierten Fettkörperzellen, welche gelborange Lipidtröpfchen enthalten. Da das Vorhandensein der Flecken geschlechtsspezifisch ist, ihre Ausdehnung (die auf beiden Seiten unterschiedlich sein kann) zudem positiv mit der Pronotumbreite korreliert ist und ihr Farbton offenbar von einer carotinoidreichen Nahrung abhängt, vermuten wir in ihnen ein konditionsabhängiges Merkmal, das eine Rolle bei der Partnerwahl und/oder bei der intraspezifischen Aggression spielt, aber auch als Warnsignal dienen könnte.

Schlüsselwörter: Balz und Paarung, Pronotum, Asymmetrie, konditionsabhängiges Merkmal, Carotinoide, Fettkörper

1. Introduction

South American cockroaches of the genus *Lucihormetica* are noticeable animals. They are viviparous (for terminology see Greven 1979; for a more complex terminology see Bell et al. 2011), nocturnal, and their pronota show a remarkable sexual dimorphism: Males possess two prominent, usually yellows spots, which fade in specimens stored in ethanol. The genus with the species *L. fenestrata* was first described by Zompro & Fritzsche 1999), who considered the two pronotal spots (more or less from hearsay) as luminescent organs. Since then, in original articles and textbooks *Lucihormetica* spp. were considered as unique among hemimetabolous insects due to their bioluminescence. However, neither bioluminescence nor the structure of these spots were ever adequately documented (e. g. Zompro & Fritzsche 1999; Dettner 2003; Bell et al. 2007; Vršanský et al. 2012; Fritzsche 2013). Recently, Vršanský et al. (2012), presenting a hypothesis of the evolution of bioluminescence in insects, considered the autofluorescence of the cuticle covering the spots of *Lucihormetica* spp. as an indicator of the ability for bioluminescence. Shortly after, Merritt (2013) critically commented this interpretation and seriously disputed bioluminescence in *Lucihormetica* spp.

Strange enough, another conspicuous feature not yet considered adequately is the colour of the spot. Breeders repeatedly noted (e. g. in several internet fora) changes of the spots from yellow to bright orange or even red when males of *Lucihormetica* spp. were fed with carrots. Most recently, Fritzsche (2013) in a popular article pictured two males of *Lucihormetica subcincta*, showing this diet-depending difference. Feeding experiments being currently carried out by us confirm these observations suggesting that the expression of the spots is carotenoid-based and can be manipulated by the diet. Carotenoids are pigments of multiple functions (e. g. McGraw & Ardia 2003; Blount 2004) and carotenoid-based colours often reveal information about the nutritional state, health status, genetic quality, etc. Insects (as animals in general) are unable to synthesize carotenoids that therefore have to be ingested with food. Therefore, carotenoid-based patterns are often considered as condition-dependent traits that may play a significant role in the sexual and social context (e. g. Kayser 1982; Blount 2004; Blount & McGraw 2008).

All this prompted us to look more closely to the sexual behaviour of *L. verrucosa* and the pronotal spots of the males. In the present article we therefore (i) document courtship and mating of *Lucihormetica verrucosa*, a glowspot cockroach from Venezuela and Colombia, (ii) examine the variability of the pattern of the pronotum and document asymmetries of the yellow spots, and (iii) describe the structure of the spots by histological sections and scanning electron microscopy providing a basis for further studies on the significance of these noticeable markings.

2. Material und Methods

2.1. Origin and keeping of the cockroaches

We received approximately 45 specimens of *Lucihormetica verrucosa* of various developmental stages from a private breeder. Male and female nymphs were separated and kept at 26-28 °C in transparent plastic containers (15 x 10 x 15 cm) with small holes and equipped with a 5 cm layer of wet peat and some earthenware as shelters. Nymphs were fed with dog food, sticks for fish, bread, oat flakes and fresh fruits and vegetables. Nymphs were daily checked for imaginal moult.

2.2. Behavioural observations

We conducted 24 trials using nine combinations of virgin females and virgin males. Pairs were arranged from five virgin females (30 min to 26 d after the imaginal moult) and seven virgin males (6 h to 17 d after imaginal moult) (Tab. 1). *Lucihormetica hormetica*-specimens are fully coloured 4-5 hours after the final moult, but still softer than fully sclerotized specimens, which process takes a longer time (ca. 6-8 h).

For observations and photographs a couple was placed in a plastic container (9.5 x 6 x 9.5 cm) on a piece of white carton without substrate and top. The inner walls of the container were covered with Vaseline to prevent flight. A 20 W halogen lamp illuminated the container from the top. Temperature was approx. 26 °C. Photos were taken with a digital camera (Fa. Panasonic: Lumix, DMC-TZ7; lens: DC Vario-Elmar; 4.1-49.2 mm; 1:3.3-4.9; Fa. Leica).

During observations we noted (i) the time until the male started courtship, i. e. when he touched the female for the first time with his antennae; (ii) responses of the female; (iii) the time when copulation started, i. e. when partners were connected and their heads showed in opposite directions; (iv) duration of the copulation, i. e. until mates separated. Time was measured with a digital stop-watch.

Duration of the trials depended on the behaviour of the animals. When female and male did not show any courtship behaviour, the trial was stopped after 15 min. In case only the male or male and female showed elements of courtship display but did not copulate, the test was stopped after 30 min. If mates copulated, they were observed until their final separation. Females that did not mate with a given male were offered a second male within 30 min.

2.3. Variability of the pronotum

We measured total length of 11 males (from anterior margin of the pronotum to the end of the abdomen) and width of the pronotum with a calliper. Further, we photographed the pronota of 27 adult males and some nymphs and adult females. Specimens were held at a distance of 2.8 cm from the lens of the above mentioned digital camera fixed on a tripod. The photos were used to measure the width of the pronotum, the areas of the yellow spots and the surrounding russet areas with a specific program (Olympus DP-Soft, Version 3.1). The values obtained in pixel were converted in absolute distances and areas, respectively. Statistical tests (D'Agostino-Pearson- and Shapiro-Wilk-Test) to test normal distributions of the values obtained from the left and the right side, paired and unpaired t-test to show differences between the yellow spots and correlation analyses after Pearson) were performed using GraphPad Prism, Version 6.0. Diagrams and trend lines were drawn with Exel 2000. We tentatively determined the index of fluctuating asymmetry (= FA defined as small random deviations from perfect symmetry in bilateral traits; LUDWIG 1932) of the spots as their unsigned right-minus-left difference (PALMER & STROHBECK 1986).

2.4. Organisation of the pronotum

2.4.1. Light microscopy

Two pronota were removed from fully sclerotised males, macerated in 10 % KOH, washed in aqua dest. and viewed in transmitted light. Parts of freshly excised pronota and some pieces of the KOH-treated material were fixed in 2.5% glutaraldehyde (GA) in 0.1 mol/l cacodylate buffer, postfixed in 1% osmiumtetroxide in the same buffer, dehydrated and embedded in Spurr's resin (SPURR 1969). Semithin sections (1-1.5 µm thick) were stained with toluidine blue/borax.

2.4.2. Scanning electron microscopy (SEM)

Whole pronota were fixed in GA (see above), dehydrated in an ethanol series, transferred in liquid nitrogen, split longitudinally with a razor blade and finally critical-point dried Specimens were glued on metallic stubs, sputtered with gold, and viewed in a SEM Leo 1430 (Fa. Zeiss).

3. Results

3.1. Courtship and mating

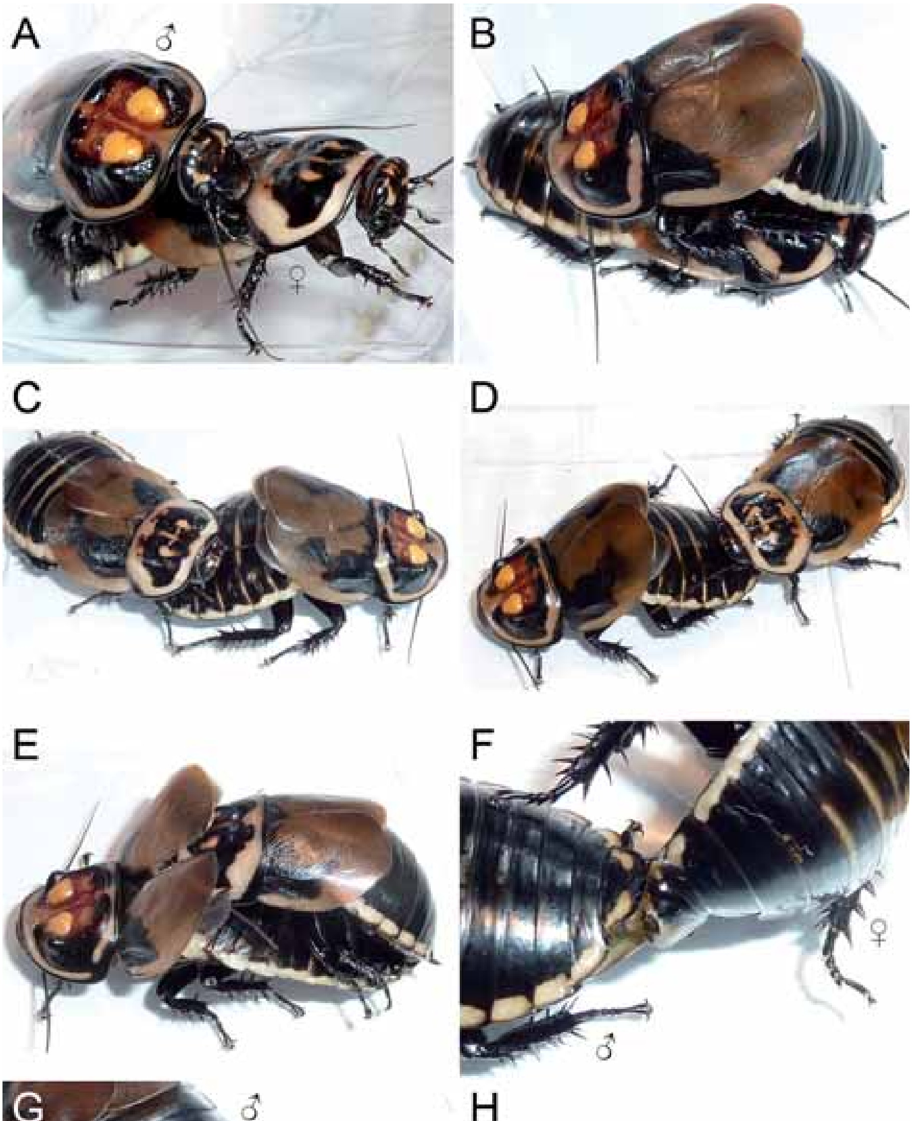
We recognized the following behavioural elements during courtship and mating: The male (1) palpates the female with his antennae and (2) then with his palps; (3) pursues the female; 4) pushes the female away (in front of him); (5) climbs the female; (6) raises his wings**.** The female (1) may escape; (2) may be restrained; (3) allows the male to push her away; (4) palpates his abdomen with her maxillary and labial palps; (5) climbs on the male's dorsum, get off laterally and allows mating (or not).

3.1.2. Males

In 21 trials courtship began at different times ranging from 9 s to 8:15 min. Obviously there was no connection between the age of the animals and the time the courtship started (not shown). In three trials, females (5, 10 und 20 d after imaginal moult) palpated the abdomina of the more or less restlessly moving males (6 h, 8 h and 6 d after imaginal moult), but no further courtship display was seen. In the majority of trials (20) courtship was opened by the males stroking the female's body with their antennae (Fig. 1 A). In one trial the female opened the courtship palpating the male's abdomen with her palps. In 21 trials the male palpated body regions (pronotum, forewings or elytra, abdomen, genital region) of the female with his maxillary and labial palps (Fig. 1 A). In eight trials males completely climbed upon the female (Fig. 1 B). In six trials the male followed the female that walked through the container trying to palpate her abdomen. In 19 trials the male near the female raised his forewings and hind wings at approx. 90°. Thereby he turned his abdomen towards the female's head (Fig. 1 C, D) arching his body using his legs, especially the second pair, and the abdomen. With this posture the male invited the female to climb on

Fig. 1: Courtship and mating in *Lucihormetica verrucosa*. The male stimulates the female with his palps and antennae (**A**), mounts the female (**B**), "invites" her raising the wings (**C**, **D**); the female climbs on the male and he clasps her genitalia (**E**), the female dismounts the male rotating 180 degrees (**F**, **G**); mates reach the final position. (**H**).

Abb. 1: Balz und Paarung bei *Lucihormetica verrucosa*. Das Männchen berührt das Weibchen mit seinen Palpen und Antennen (**A**), klettert auf das Weibchen (**B**), bietet sich diesem mit gehobenen Flügeln an (**C**, **D**); das Weibchen steigt auf das Männchen und dieses stellt den Genitalkontakt her (**E**); das Weibchen steigt dann ab und dreht sich dabei (**F**, **G**), bis die endgültige Kopulationsstellung erreicht ist (**H**).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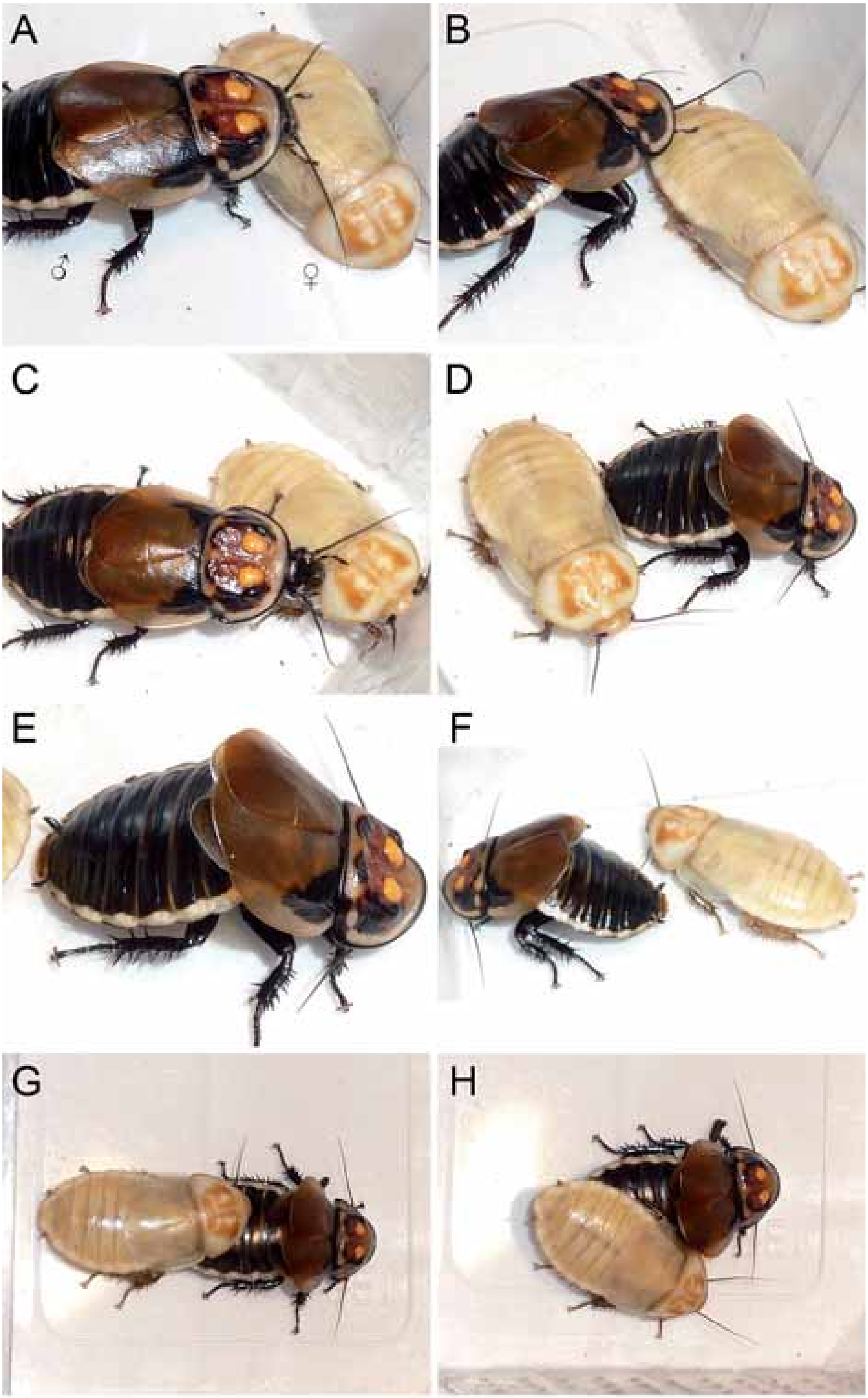
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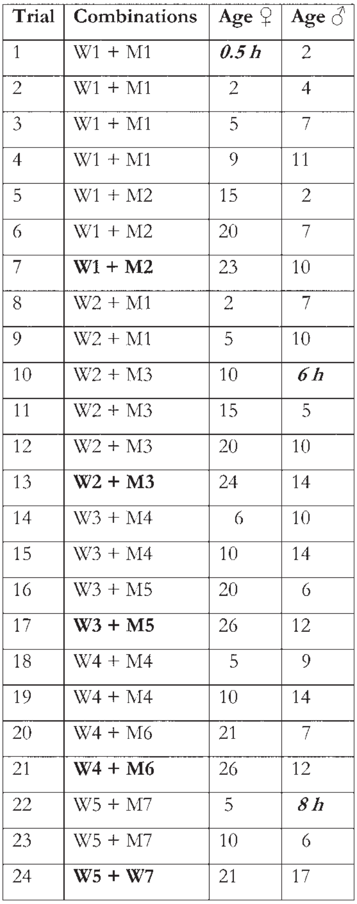
his dorsum. If the female did not mount the male, he lowered the wings and again palpated the female with his antennae and palps. Inviting posture and palpation may alternate several times. Although females immediately after the imaginal moult are not receptive, males courted her (palpation, inviting posture) (Fig. 2).

3.1.3. Females

In the 12 trials without copulation, females were restrained already at the beginning and responded defensively to the palpation of males. They remained motionless retracting head and antennae under the pronotum; occasionally they put the legs against the body pressing the abdomen against the substrate (see Fig. 2 A, B). In eleven trials the previously restrained females became more active later and responded to the inviting posture of the males by palpating their abdominal and genital region. In nine trials females climbed upon the male palpating his body (Fig. 1 E), but then dismounted the male and did not permit copulation.

Tab. 1: Combinations of females and males of *Lucihormetica verrucosa* and their age (in days after final moult) used for courtship and mating trials. Combinations with copulations in bold. Age = hours (italic letters) or days after imaginal moult.

Tab. 1: Paarkombinationen von Weibchen und Männchen von *Lucihormetica verrucosa* für die Versuche zur Balz und Paarung. Fett: Kombinationen mit Kopulation. Alter = Stunden (kursiv) oder Tage nach der Imaginalhäutung.



Trial	Combinations	Age ♀	Age ♂
1	W1 + M1	***0.5 h***	2
2	W1 + M1	2	4
3	W1 + M1	5	7
4	W1 + M1	9	11
5	W1 + M2	15	2
6	W1 + M2	20	7
7	**W1 + M2**	23	10
8	W2 + M1	2	7
9	W2 + M1	5	10
10	W2 + M3	10	***6 h***
11	W2 + M3	15	5
12	W2 + M3	20	10
13	**W2 + M3**	24	14
14	W3 + M4	6	10
15	W3 + M4	10	14
16	W3 + M5	20	6
17	**W3 + M5**	26	12
18	W4 + M4	5	9
19	W4 + M4	10	14
20	W4 + M6	21	7
21	**W4 + M6**	26	12
22	W5 + M7	5	***8 h***
23	W5 + M7	10	6
24	**W5 + W7**	21	17

3.1.4. Copulation

Copulations were observed, always after courtship, in five trials. All females permitting copulation had shed finally at least 20 days before and, therefore, were fully sclerotized (Tab. 1). One female mated with the first male offered to him, and four females with the second male. When the female was on the male, he made genital contact while raising his wings (Fig. 1 E). For that he moved backwards griping the female's genitals with

Fig. 2: Courtship and mating in *Lucihormetica verrucosa* with a female still pale and teneral white 30 min after the imaginal moult. The male palpates the impassive female that flattens herself against the substratum tucking legs and antennae under the body (**A**, **B**), the female becomes more active, and the mail raises his wings presenting the dorsal surface of the abdomen (**C**-**F**), the female climbs on the dorsum of the male(**G**), but dismounts him again (**H**).

Abb. 2: Balz eines *Lucihormetica verrucosa*-Männchens mit einem noch blassen, zarten Weibchen 30 min nach der Imaginalhäutung. Männchen betastet das teilnahmslose Weibchen, das sich gegen den Boden drückt und Antennen und Beine unter dem Körper versteckt (**A**, **B**), Weibchen wird aktiver, Männchen bietet sich an (**C**-**F**), Weibchen klettert auf das Männchen (**G**), steigt aber wieder ab (**H**).

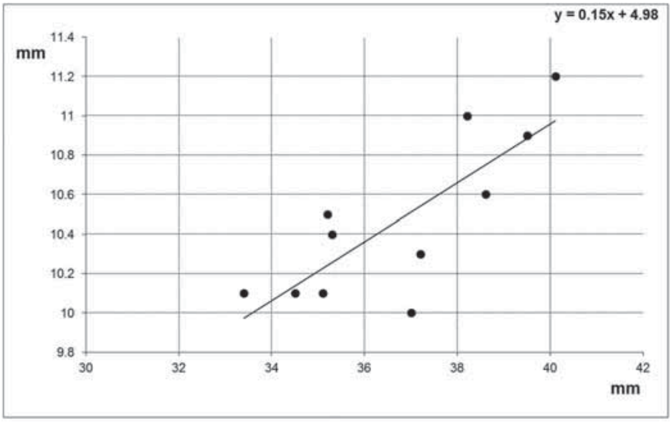


Fig. 3: Linear relationship between the width of the pronota (ordinate) and the total lenght (abscissa) of 11 males of *Lucihormetica verrucosa*; r = 0.7985; p = 0.0032.
Abb. 3: Beziehungen zwischen der Weite des Pronotums (Ordinate) und der Gesamtlänge (Abszisse) bei elf Männchen von *Lucihormetica verrucosa*; r = 0,7985; p = 0,0032.

the genital hawk. To achieve the final position for copulation, the female dismounted the male and turned around at approx. 180°. After that mates are in a linear opposed position (Fig. 1 F, G, H). Duration of copulation varied between 45:00 und 74:02 min.

The time, the copulation started, i. e. the partners had taken the final position and the phallomers had been inserted, varied between 04:59 und 12:14 min. In one trial the pair definitely joined twice for five and seven seconds, but did not reach the final positions. Later they copulated for 62.19 min. The longer the time until copulation took place, the more often males performed courtship display; especially he adopted the inviting posture and palpated the female. In the first 5 to 10 min of the copulation males appeared somewhat restless, twitching with their abdomina and legs. In this phase the couple may slightly move, but later mates did not change their position; occasionally they cleaned their antennae.

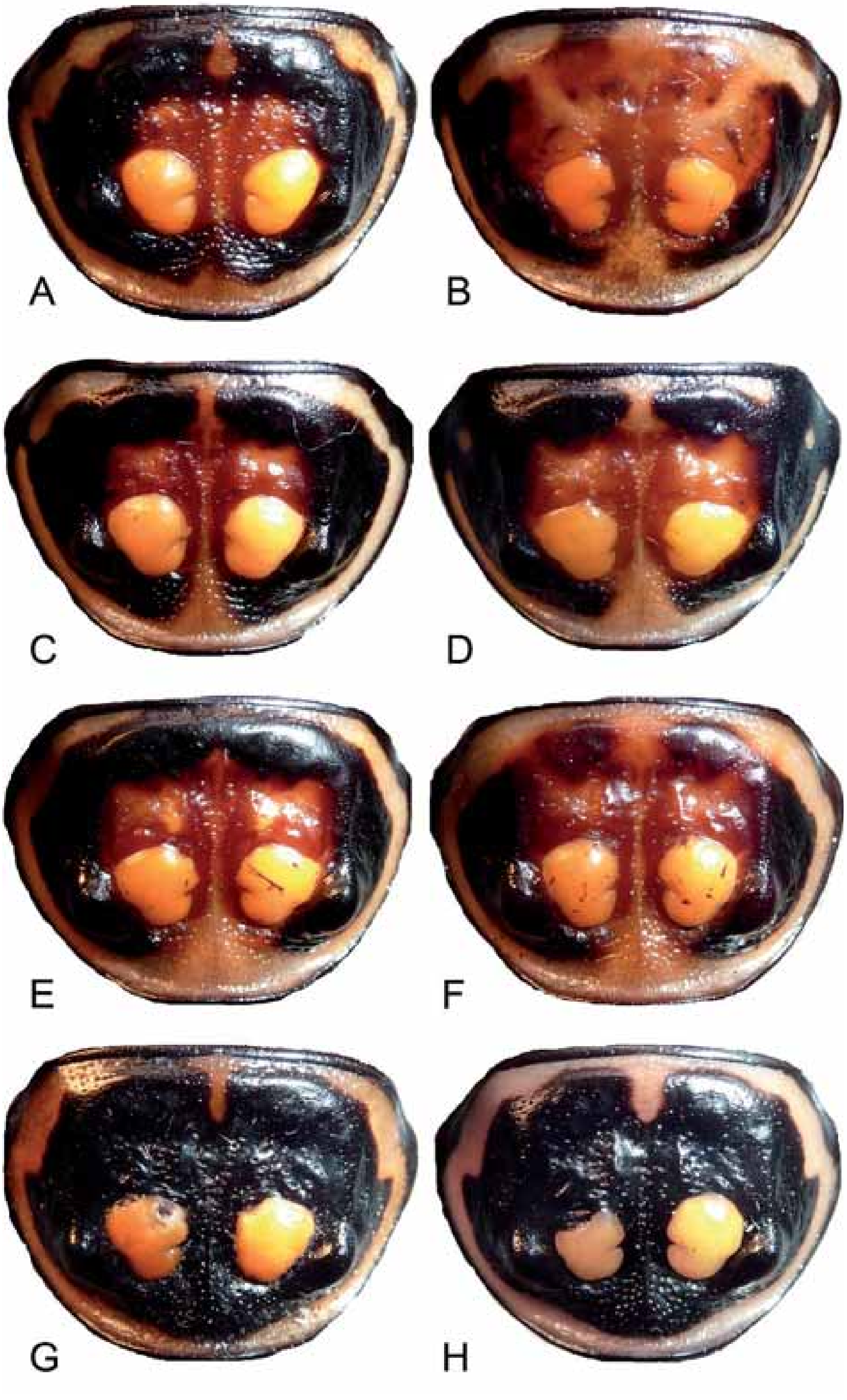
In four trials the male turned towards the female immediately after separation of the couple, palpating her pronotum, wings and abdomen for a short time, whereas in the other trials males ignored the females. In one trial the male took the inviting posture a few seconds after the copulation.

3.2. Variability of the pronotum

3.2.1. Size and colouration of the male pronotum

Relationship between pronotum width and total length of the males is linear (Fig. 3). The mean width of the pronota of 27 males was 11.35 ± 0.66 (range: 9.63 to 12.53 mm). In 25 from 27 males pronota showed four differently coloured areas (Fig. 4 A, C, D, E): (i) two distinct yellow spots in the middle of the anterior half of the pronotum, which are smooth, notched at their inner sides, elevated and slightly variable in their shades; (ii) a

Fig. 4: Variability (**A-H**) of the colour pattern of the pronotum of male *Lucihormetica verrucosa*. Note slight and distinct asymmetries of yellow spots.
Abb. 4: Variabilität (**A-H**) des Farbmusters auf den Pronota einiger Männchen von *Lucihormetica verrucosa*. Man beachte die z.T. deutliche Asymmetrie der gelben Flecken.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bilateral, roughly crescent-shaped more or less uneven, black area encircling the spots anteriorly, laterally and posteriorly (here occasionally incomplete; see Fig. 4 B, F); in this area a black tubercle adjacent to each spot is present anteriolaterally; (iii) a russet area that anteriorly bears the yellow spot and is sagitally crossed by a brighter furrow that cut the pronotum in halves. The deepening often widens anteriorly and may be on both sides continuous with (iv) the ivory-coloured border of the pronotum (for details and deviation from this pattern, see Fig. 4). Remarkably, in two males the russet area was completely black (Fig. 4 G, H). In one of these males the posterior extension of the left spot was reduced posteriorly (Fig. 4 H).

The area of the left spot was 6.39 ± 1.07 mm^2 on average covering the range from 3.73 to 7.84 mm^2. The second smallest spot measured 5.04 mm^2. The area of the right spot was 6.35 ± 0.9 mm^2 (range 4.01-8.03 mm^2). The gap between the smallest (4.01 mm^2) and the next largest spot (4.98 mm^2) was somewhat smaller.

Figure 5 shows that the larger the pronotum, the larger are the areas of the spots (Fig. 5 A-C). Therefore, the male with the smallest width of the pronotum (9.63 mm) had the smallest spots (left: 3.73 mm^2; right: 4.01 mm^2). Larger variations (left spot: 5.5 to 8.0 mm^2; right spot: 5.5 to 7.7 mm^2) were recognized between a pronotum width of 11.3 and 12.0 mm. The largest variation was found in the male with the reduced spot (see Fig. 4 H). The left spot measured 5.18 mm^2, the right spot 7.59 mm^2, and the width of the pronotum, the largest in our samples, measured 12.53 mm.

Differences between the left and right spot as well as those of the large and small spots, (independent of their position on the right or left side) are not identifiable with conventional statistics. In the first case p is 0.67 (paired t-test), in the second case 0.28 (unpaired t-test) (large spots; 6.52 ± 0.2 mm^2; small spots: 6.22 ± 1.95 mm^2, N =27). The index of fluctuating asymmetry was relatively high (mean value of all males 0.3 ± 0.45; range 0.01-2.41; without the "aberrant" male 0.22 ± 0.17; range 0.01-0.78). The russet and black areas do not show any relationship to the width of the pronotum (not shown).

3.2.2. Structure of the pronotum cuticle and the underlying tissue

The various areas of the pronotum reveal different surfaces in SEM micrographs. At lower magnification the surfaces of the cuticle covering the yellow spot and the associated black tubercles appear smooth. However, the latter, the surrounding cuticle of the russet area and the furrow between the spots show small depressions, whereas the yellow spot shows irregularly arranged small knobs (Fig. 6 A, B). Each depression and each knob bear a short "hair", probably a mechanoreceptor (Fig. 6 C, D). Outside of the depressions very small "sensory hairs" are present (Fig. 6 D, E). Generally, the entire surface shows small polygonal to rounded "scales" that appear slightly elevated over the yellow spots (Fig. 6 C; see also Fig. 6 F, 8 D). Pores of epidermal gland cells are practically absent on the spots, but numerous in the surrounding cuticle (see Fig. 6 D, E). The undersurface of the free edge of the pronotum bears long, probably tactile "hairs" (not shown).

In contrast to the surrounding cuticle, the cuticle of the yellow spots is transparent, which is clearly seen preparations, in which the soft tissue was removed by KOH-treated samples. Sections show that in this area the exocuticle is highly reduced (Fig. 7 A, B). Both, the transparent and non-transparent cuticle typically consist of the epicuticle (considerably thick only in the cuticle surrounding the spot), the exocuticle and the endocuticle; in the latter the typical lamellation is clearly apparent. The underlying epidermis is single-layered (Fig. 8 A-D). Gland

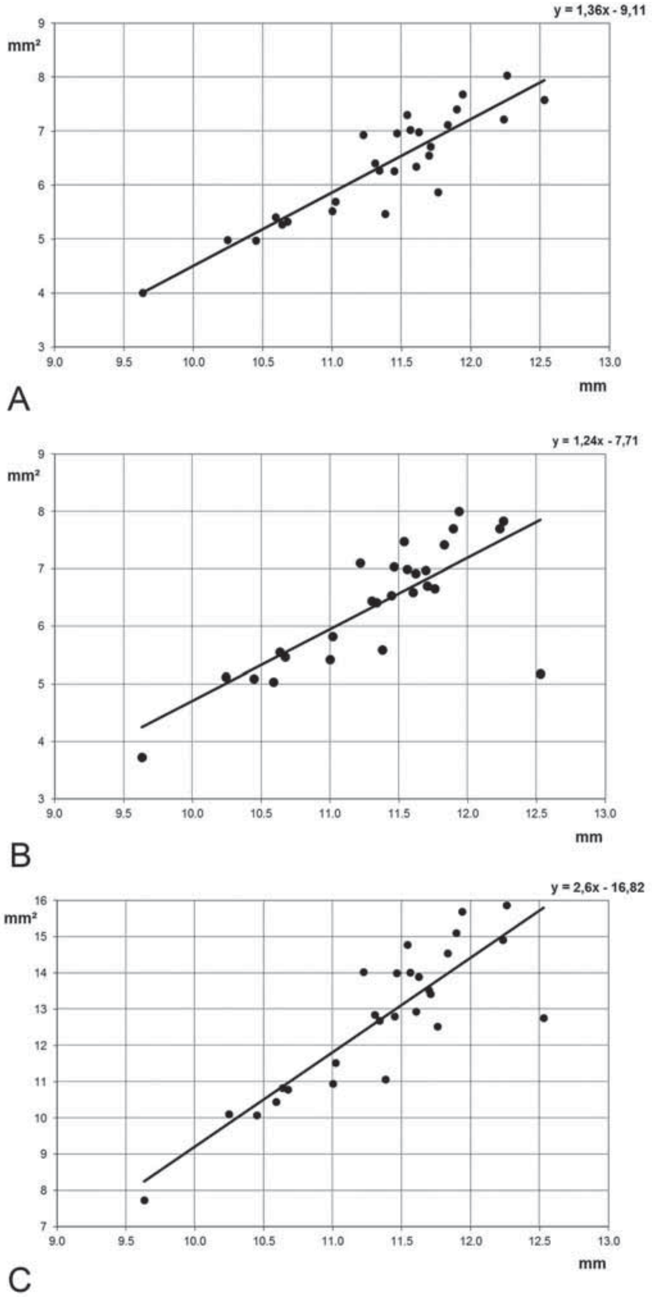

Fig. 5: Linear relationships between the width of the pronotum (abscissa) and size of the yellow spots (ordinate) in 27 males of *Lucihormetica verrucosa*. **A** Right spot; r = 0.9027; p < 0.0001. **B** Left spot; r = 0.7668; p < 0.0001. **C** Both spots; r = 0.8625; p < 0.0001.

Abb. 5: Lineare Beziehungen zwischen der Weite des Pronotums (Abszisse) und der Größe der gelben Flecken (Ordinate) bei 27 Männchen von *Lucihormetica verrucosa*. **A** Rechter Fleck; r = 0,9027; p < 0,0001. **B** Linker Fleck; r = 0.7668; p < 0,0001. **C** Beide Flecken; r = 0.8625; p < 0.0001.

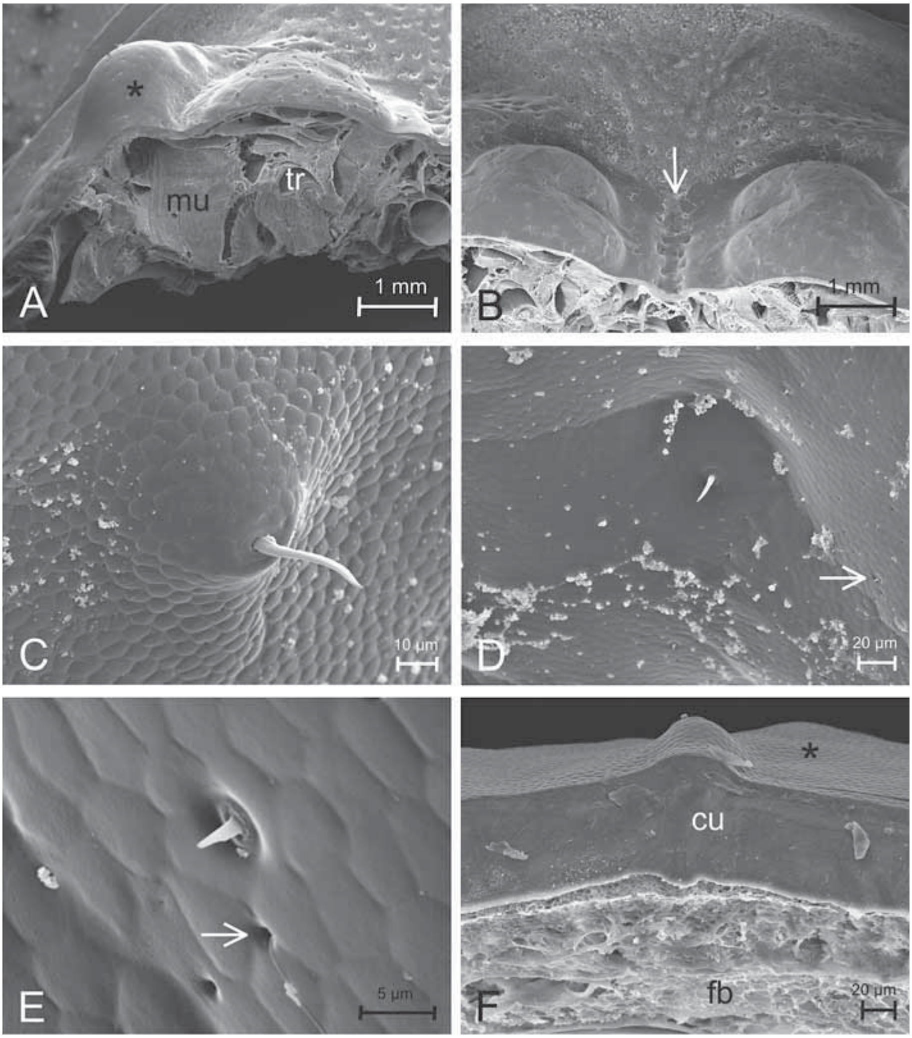

Fig. 6: SEM of the male's pronotum of *Lucihormetica verrucosa*. **A** Lateral tubercle (asterisk) and adjacent slightly elevated yellow spot with small protuberances (right side). **B** The two yellow spots, the medial furrow (arrow) and part of the russet area (on the top) with small depressions (above). **C** Sensory "hair" on a knob of the yellow spot. Note the "scale"-like (rippled) surface structure. **D** Sensory "hair" in a depression of the russet area (see also B). Note the small sensory "hair" (arrow) outside the depression and adjacent pores. **E** Higher magnification from D. Sensory "hair" and openings (pores) of epidermal gland cells (arrow). **F** Fractured plane of the yellow spot with lamellated cuticle. Note the rippled surface of the cuticle (arrow); fb = fat body; mu = muscles; tr = trachea.
Abb. 6: SEM des Pronotums eines Männchens von *Lucihormetica verrucosa*. **A** Seitliche Ausbuchtung (Stern) und leicht erhabener gelber Fleck mit kleinen Protuberanzen (rechts). **B** Die beiden gelben Flecken, die mittlere Rinne (Pfeil) und Teil des rotbraunen Bereichs (oben) mit kleinen Vertiefungen. **C** Sinnes„haar" auf einer Protuberanz des gelben Flecks. Man beachte die Skulpturierung der Cuticula. **D** Sinnes„haar" in einer Vertiefung der rotbraunen Bereichs (siehe auch B) mit einem weiteren kleinen Sinnes„haar" außerhalb der Vertiefung und benachbarten Poren. **E** Vergrößerung aus D. Sinnes„haar" und Öffnungen von epidermalen Drüsenzellen (Pfeil). **F** Bruch durch einen gelben Fleck mit lamellierter Cuticula. Man beachte die Skulpturierung der Cuticula-Oberfläche (Pfeil). fb = fat body; mu = muscles; tr = trachea.

cells that open to the exterior via small pores appear to be rare, if at all they are present in the spot-cuticle. Immediately beneath the epidermis a thick cushion of large cells is located, which contain yellow-orange droplets after toluidine blue staining. In unstained sections this colouration is less conspicuous. In this area also several tracheae of variable calibers are seen (Fig. 8 A, E).

3.2.3. The pronotum of nymphs and females

Contrary to males, females and nymphs do not have tubercles and yellow spots on their pronota. In nymphs of both sexes pronota are black except of two light marginal spots. In the course of subsequent moults further light spots, including the future yellow spots, develop (Fig. 9 A-D). Females' pronota exhibit a black pattern in the midst of each pronotum with ivory-coloured patches at the site, where males have the yellow spots (Fig. 9 E, F).

4. Discussion

4.1. Courtship and mating

Courtship and mating have been extensively described for many cockroach species (e. g. summarized in Schal et al. 1984; Sreng 1993; Bell et al. 2007, with a wealth of references). Therefore we only discuss herein some selected traits.

Contrary to other Blaberidae such as *Diploptera punctata* and *Eublaberus posticus*, whose females are receptive and mate just after the final moult before the cuticle has hardened, freshly emerged females of *Lucihormetica verrucosa* are courted, but do not accept mates. They flatten themselves against the substratum with their legs and antennae tucked under the body to signal non-receptivity. Obviously females need some days to become willing to copulate as known from other Blaberidae, e. g. from *Nauphoeta cinerea*, one of the best-studied cockroaches. Under the conditions we kept *L. verrucosa* this delay was approx. 20 days.

Precopulatory and copulatory behaviour of *L. verrucosa* largely corresponds to the "type I mating behaviour", which includes (largely adopted from Bell et al. 2007) (i) orientation to a potential mate; (ii) mutual stimulation with the antennae and palps (during this phase males of *L. verrucosa* did not seem to specifically expose their spots, but, nevertheless, females may perceive these signals during these actions; however, fighting males typically lower their pronota

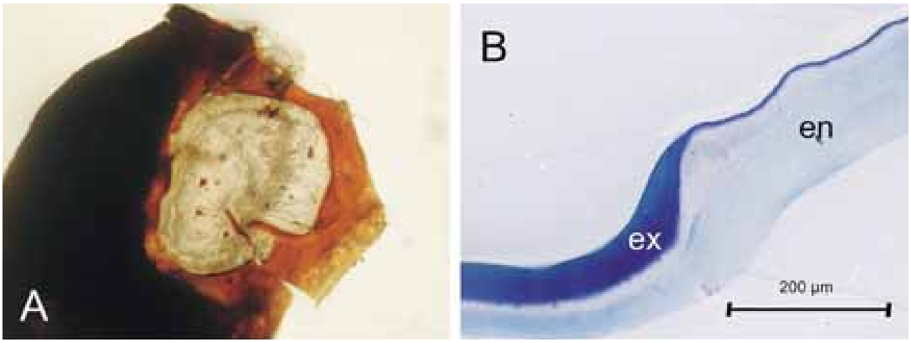

Fig. 7: Pronotum of a male of *Lucihormetica verrucosa* after KOH-treatment. **A** Part of the pronotum with the translucent cuticle covering the yellow spot. **B** Histological section; the exocuticle (ex) of the spot-cuticle (right side) is highly reduced; en = endocuticle.

Abb. 7: Pronotum eines Männchens von *Lucihormerica verrucosa* nach KOH-Behandlung. **A** Teil des Pronotums; die den gelben Fleck bedeckende Cuticula ist durchsichtig. **B** Histologischer Schnitt; die Exocuticula (ex) der Cuticula über dem „gelben Fleck" ist stark reduziert; en = Endocuticula.

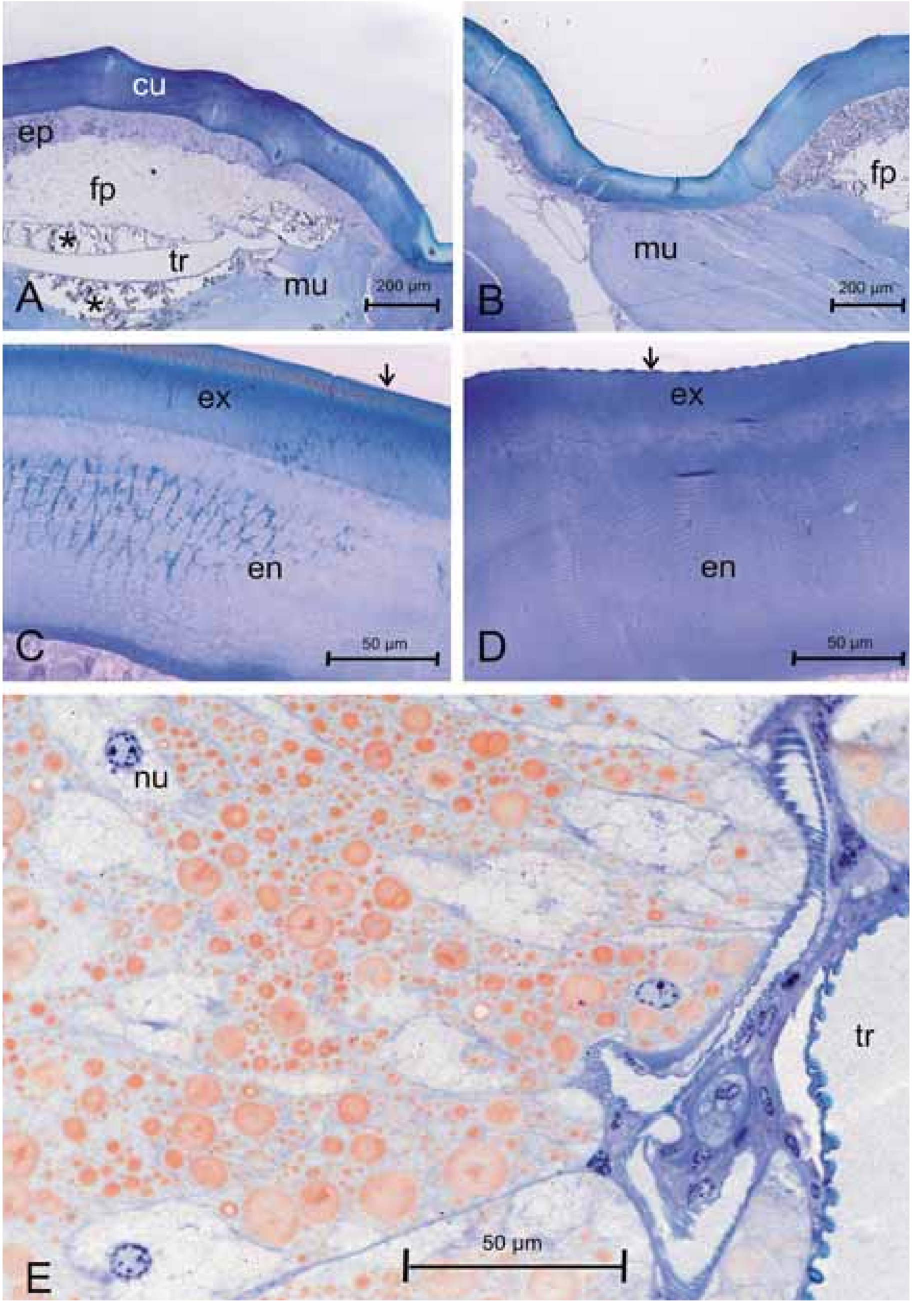

Fig. 8: Histology of the pronotum of males of *Lucihormetica verrucosa*, transverse sections: **A** Elevated yellow spot. Note the relatively thick cuticle (cu), the epidermis (ep) and the subepidermal pad of fat body cells (fp). Artifacts (asterisks). **B** Transition (middle) to the black tubercle (left side). **C** Cuticle covering the black tubercle; note the strong epicuticle (arrow) as well as exo- (ex) and endocuticle (en). **D** Cuticle covering the yellow spot. Note the rippled thin epicuticle (arrow). **E** Detail of the subepidermal fat body. The hypertrophied cells contain numerous yellow-orange

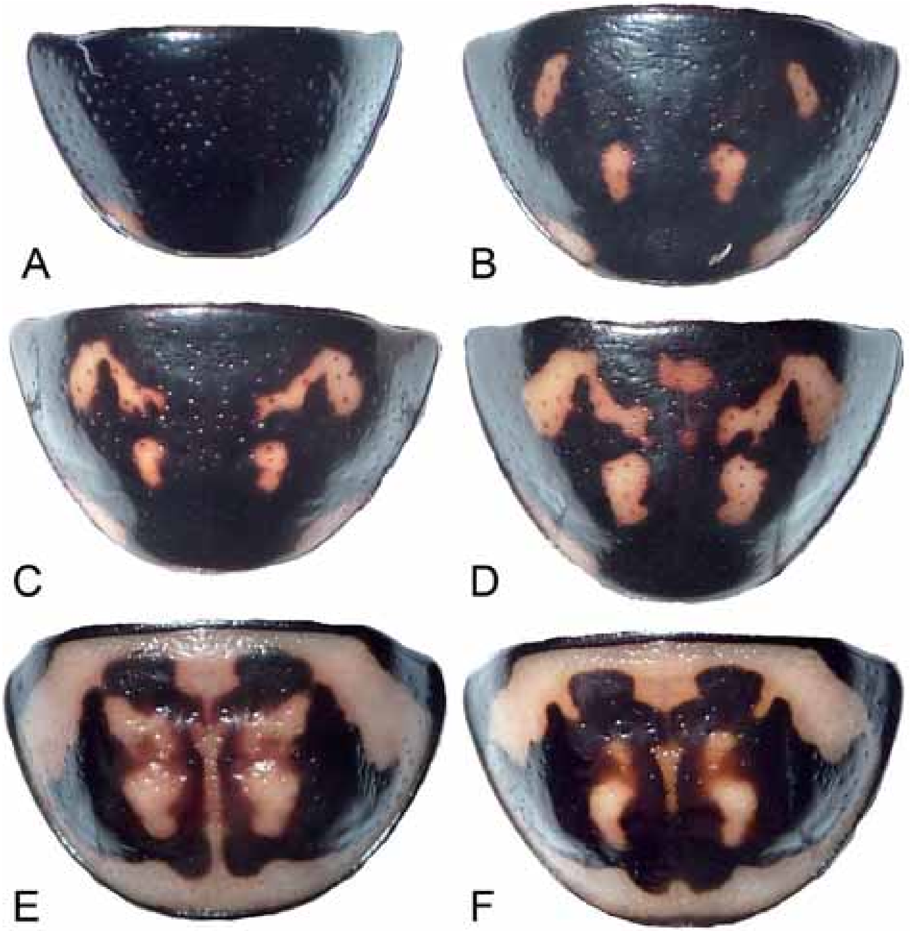

Fig. 9: A-D Colour-markings of the pronota of various developmental stages in male nymphs of *Lucihormetica verrucosa*. The colour of the later yellow spots (in B) does not differ from other markings in nymphs. **E**, **F** Pronota of two adult females with ivory-coloured markings.

Abb. 9: A-D Farbmarkierungen der Pronota verschiedener Nymphenstadien (Männchen) von *Lucihormetica verrucosa*. Die späteren gelben Flecken (s. B) heben sich bei Nymphen noch nicht deutlich von anderen Farbmarkierungen ab. **E, F** Pronota zweier adulter Weibchen mit elfenbeinfarbenen Markierungen.

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lipid droplets; en = endocuticle; ep = epidermis; ex = exocuticle; cu = cuticle; fp = pad of fat body cells; mu = muscles; nu = nucleus; tr = trachea.

Abb. 8: Histologie des Pronotum der Männchen von *Lucihormetica verrucosa*; Querschnitte. **A** Erhöhter gelber Fleck. Man beachte die relative dicke Cuticula, die Epidermis (ep) und das subepidermale Polster von Fettkörperzellen (fp). Artefakte (Sternchen). **B** Übergang (Mitte) zur dunklen Vorwölbung (links). **C** Cuticula des schwarzen Höckers neben dem gelben Fleck. Man beachte die kräftige Epicuticula (Pfeil) sowie Exo- (ex) und Endocuticula (en). **D** Cuticula über dem gelben Fleck. Man beachte die wellige Epicuticula (Pfeil). **E** Detail aus dem subepidermalen Fettkörper-Polster. Die hypertrophierten Zellen enthalten zahlreiche orangefarbene Lipidtropfen; en = Endocuticula, ep = Epidermis, ex = Exocuticula; Cu = cuticula; fp = Fettkörper, mu = Muskeln; nu = Zellkern; tr = Trachee.

in front of the rival (as do many other cockroaches) exposing their yellow spots); (iii) the male of *L. hormetica* often mounts the female (not mentioned in Bell et al. 2007 for type 1); (iii) the male presents the dorsal surface of his abdomen by rising the wings (males of *L. hormetica* never flapped with the wings as other Blaberidae, but hold them up until the female climbed onto his back); (iv) the females climb on the dorsum of the male and probably "feed" on secretions of the male's tergal glands (The fact that in 23 of 24 trials females of *L. hormetica* palpated the male's abdomen may suggest the presence of tergal glands; however, according to the literature (Bell et al. 2007) tergal glands are said to be rare in Blaberidae being probably absent in members of the subfamily Blaberinae); (v) the male backs up clasping her genitalia; (vi) the male moves forward, the female rotates 180° and mates reach the final linear opposed position.

How and to which extent contact pheromones and short- or long-distance volatile attractants emitted by the mates are involved in mate finding, courtship and mating (see Gemeno & Schal 2004) is not explored in *L. verrucosa*, but occasional observations seem to indicate that neither males nor females attract partners by pheromones acting over long distances. In the context of non-chemical cues (e. g. tactile and acoustic signals) used to find mates, Bell et al. (2007, p. 91) also touch on *L. hormetica* with their "pronotal headlights" assuming that "even nocturnally active cockroaches may use sight in attraction or courting mates" as suggested by Zompro & Fritzsche (1999), but Bell et al. (l. c.) add the note that "live material had never been examined".

Generally, females decide on the course of courtship and copulation and can break off the action in every phase often without obvious reasons (Bell et al. 2007). This holds also for females of *L. verrucosa*. In nine trials females palpated the male's abdomen and then turned away and in further nine trials they climbed onto the male without permitting copulation.

4.2. Structure and possible significance of the pronotum and the yellow spots

Pronota of adult cockroaches are notably diverse reflecting their various functions. They may serve as shields, shovels, battering rams etc. and may even serve in acoustic and tactile communication (s. Bell et al. 2007). Sexually dimorphic pronota are known from several genera: Males may have for instance pronotal knobs, tubercles, horn-like processes, etc. These structures are considered as arms related to (sexual) competition among males (summarized in Bell et al. 2007). The tubercles of the pronotum of the highly aggressive males of *Lucihormetica verrucosa* may be also useful in this context.

Sexually dimorphic pronota that differ in colour patterns appear to be rare among cockroaches and the two yellow spots seem to be a unique feature in *Lucihormetica* spp. As already mentioned (see introduction), the assumption that these spots are luminescent organs attracting females during night (Zompro & Fritzsche 1999), illuminating the nearby environment and mimicking syntopic poisonous click beetles of the genus *Pyrophorus*, which have similarly arranged true luminescent organs (Vršanský et al. 2012), was neither supported by direct observations nor by experimental work with living specimens. Further, the conclusions concerning bioluminescence and mimicry the authors drew from the comparison of the optical properties of the "lanterns" of *L. verrucosa* and a museum species of *Lucihormetica luckae* with those of the light organs of the elaterid *Pyrophorus noctilucus* and the lampyrid *Lampyris noctiluca* as well as purified commercial luciferin were seriously questioned (see Merritt 2013).

Regarding the structure of the yellow spots, we were unable to confirm the findings of Vršanský et al. (2012). Authors using the non-invasive µ-Ct describe the structure of the "lantern" as "extremely sophisticated", its cuticle as a "bilayer of chitin net with a strong supporting function" and "the surface of the lantern" as "extremely modified, covered by a film of transparent reflector-like structure" (Vršanský et al. 2012, p. 743). Rather we have shown here with SEM and LM that the cuticle covering the entire pronotum typically consists of the epicuticle, the exocuticle (extremely reduced in the unpigmented cuticle covering the spots, which therefore is highly translucent) and the clearly lamellated endocuticle (for details regarding the insect cuticle see e. g. Hepburn 1985). Surface sculpturing of this cuticle slightly differs from the rest of the pronotum, but its surface is not highly porous as suggested by Zompro & Fritzsche (1999), as the number of secretory cells in the epithelium beneath the cuticle, which open to the exterior via pores, is limited.

Zompro & Fritzsche (1999, p. 215) characterised the yellow spots as "kidney-shaped, with a sponge-like internal structure. The interior seems to be connected with the outside by a lot of small pores which probably serve for gaseous exchange", but did not further specify this matter. The figure 1l in Vršanský et al. (2012), which shows a "non-destructive 3D µCT … section of luminescent lantern", is hardly to interprete, because any details are missing (p. 741).

We think the tissue underlying the spot is a cushion of fat body cells, mainly adipo- or trophocytes that are hypertrophied and crowded with carotenoid-containing lipid droplets. Droplets stain slightly blue after Nile Blue indicating the presence of lipids (unpublished). Accumulation of carotenoids in the fat body (for review see Dean et al. 1985; Arrese & Soulages 2010) as well as other tissues is common in insects (e. g. Wigglesworth 1972; Harashima et al. 1972; Czeczuga 1986; Eichenseer et al. 2002; Blount & McGraw, 2008). Mycetocytes containing microorganisms, as known for cockroaches, could not be clearly identified in this cushion.

The above morphological description of the yellow spots of *L. verrucosa* does not agree with the organisation of true light organs. The highly complex light organs of fireflies (Lampyridae), ontogenetically derived from the fat body, consist of "reflector cells" crowded with urate granules and a more superficial mass of large photogenic cells that is richly supplied with nerves, tracheae and tracheoles (e. g. for a concise description and review of the vast literature see Ghiradella 1998). A part of the larval fat body with luminescent adipo- or trophocytes, in which luciferin and luciferase have been demonstrated, precedes these complex organs in some lampyrids (Tonolli et al. 2011). Also in the fat body of the fungus-gnats (Mycetophilidae: Diptera) bioluminescence is generated by luciferases (e. g. Viviani 2002) and ultrastructural and biochemical studies of the larval and pupal fat body revealed specific proteinaceous granules responsible for luminescence that are missing in non-luminescent species (Baccetti et al. 1987). The only morphological traits photogenic organs and the yellow spots of *Lucihormetica* spp. have in common are the translucent cuticle ("window") overlying the spots and more or less modified fat body cells, from which almost all light organs of insects are derived (Viviani 2002). This appears too little to take at present the yellow spots for bioluminescent organs; the more so as luminescent living *Lucihormetica* spp. were never seen either in the field or in the lab. Also the demonstration of luciferases, which catalyze the reactions that produce light in bioluminescence, is missing in these species.

With the present note we mainly wanted to point to some features of the spots in *Lucihormetica* spp., which deserve closer attention in future. Spots (i) are limited to males, (ii) show a distinct relation to the size of the pronotum and, with some reservations, to the total size of the male, (iii) reveal slight asymmetries, and (iv) spot shades depend on the diet. These are reasons, to keep alive the hypothesis that the spots may play a role in social and/or sexual contexts, but without focussing on bioluminescence that currently appears less probable than ever in *Lucihormetica* spp. In view of the fact that data concerning this matter are entirely missing from both, the wild and the laboratory, we will give just a few notes and citations (mostly reviews) at this point.

Spots may have the potential to reveal information to predators, to (conspecific) rivals and/or to females. Warning of potential predators based on the size and the bright colour of the pronotum cannot be entirely excluded, but seems less probable to us. Rather we think that the spots may represent a sexually selected character, which is clearly correlated with the width of the pronotum (i. e. the larger the spots, the larger the pronotum) probably giving information about defensiveness to rivals and fitness to females already by their mere size.

A further source of information may be asymmetries. We herein tentatively determined the index of fluctuating asymmetry (FA) of the spots by a classic measure (see GRAHAM et al. 2010), primarily to point to a further example of asymmetry, a phenomenon that seems to be remarkably widespread, but seems largely unexplored in cockroaches regarding its significance (e. g. HANITSCH 1923; BELL et al. 2007; VRŠANSKÝ et al. 2012).) A detailed and sound mathematically analysis using different methods was not intended here, among others because it requires a larger number of animals (see e. g. PALMER & STROBECK 1986; HUNT & SIMMONS 1998; GRAHAM et al. 2010). FA in insects affects nearly all organs, especially genitalia (HUBER et al. 2007), as well as the number of tarsi, wing veins etc. (for cockroaches see the literature cited above). FA is often used as measure of developmental instability (reviewed in PALMER & STROBECK 1986; MARKOW 1995), but its usefulness for that was challenged more recently (DONGEN 2006). Nevertheless, it is assumed that sexually selected characters appear to demonstrate higher levels of FA than do non-sexual traits, that their degree of symmetry may be related to fitness revealing the genetic and/or phenotypic quality of individuals and, therefore, that high symmetry may correlate with male mating success (e. g. summarized in WATSON & THORNHILL 1994; MØLLER & SWADDLE 1997; MØLLER & THORNHILL 1998). This has been studied in a variety of insects, either showing such a relationship (e. g. THORNHILL 1992; MØLLER 1996; MØLLER 2001) or not (MARKOW et al. 1996). Further, asymmetrical males appear to be less successful during male-male competition (e. g. LIGGETT et al. 1993; ALLEN & SIMMONS 1996; see, however, the discussion in HUNT & SIMMONS 1998).

In vertebrates (birds and fish) carotenoid-based features are known as condition-dependent characters correlating with fitness, which give (predominantly) females an indirect measure to evaluate males (e. g. BLOUNT 2004; GRETHER & KOLLURO 2011; HILL et al. 2002). These relations are poorly studied in insects. More recently, SANDRE et al. (2007) investigating the yellow carotenoid-containing hair tufts of the larvae of the tussock moth *Orgyia antiqua* did not find relations between individual condition and variability of colouration.

Be that as it may, receiving and interpreting the yellow spots in male *L. verrucosa*, which clearly contrasts with the surrounding dark cuticle, do not necessarily require the ability of the female (and conspecific males) to perceive perfectly yellow or red shades. This ability may be somewhat reduced in nocturnal cockroaches and, thus, in *L. verrucosa* (a strictly nocturnal living of these species has still to be demonstrated). Eyes of nocturnal cockroach species (e. g. *Periplaneta americana*) are adapted to dim environments possessing two spectral receptor types with sensivity maxima at 365 and 510 nm (e. g. MOTE &

Goldsmith 1970; Mote 1990; Heimonen et al. 2006).

In sum, although *Lucihormetica* spp. are known for a while, the significance of their pronotal spots is still mysterious and awaits further studies.

Acknowledgements

We thank Dr Sascha Eilmus (Monheim), who supplied the initial stock of *Lucihormetica verrucosa*, Mr S. Köhler (Zoological Institute of the University of Düsseldorf), who assisted with the SEM, and Mrs M. Nissen (Zoological Institute of the University of Düsseldorf), who helped with the resin-embedding and semithin sections. H. G. thanks Prof. Dr K. Lunau (University of Düsseldorf) for some "illuminating" talks.

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Zeitschrift/Journal: Entomologie heute

Jahr/Year: 2013

Band/Volume: 25

Autor(en)/Author(s): Greven Hartmut, Zwanzig Nadine

Artikel/Article: Courtship, Mating, and Organisation of the Pronotum in the Glowspot Cockroach Lucihormetica verrucosa (Brunner von Wattenwyl, 1865) (Blattodea: Blaberidae). Balz, Paarung und Organisation des Pronotums der „Leuchtschabe“ Lucihormetica verrucosa (Brunner von Wattenwyl, 1865) (Blattodea: Blaberidae) 77-97