

# A Jumping Cockroach from South Africa, *Saltoblattella montistabularis*, gen. nov., spec. nov. (Blattodea: Blattellidae)

HORST BOHN<sup>1,\*</sup>, MIKE PICKER<sup>2</sup>, KLAUS-DIETER KLASS<sup>3</sup> & JONATHAN COLVILLE<sup>2</sup>

<sup>1</sup> Zoologische Staatssammlung München, Münchhausenstrasse 21, 81247 München, Germany  
[bohn@zi.biologie.uni-muenchen.de]

<sup>2</sup> Zoology Department, University of Cape Town, Rondebosch 7700, Cape Town, South Africa  
[mike.picker@uct.ac.za; jonathan.colville@uct.ac.za]

<sup>3</sup> Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde,  
Königsbrücker Landstrasse 159, 01109 Dresden, Germany  
[klaus.klass@senckenberg.de]

\* Corresponding author

Received 16.iv.2009, accepted 18.v.2009.

Published online at [www.arthropod-systematics.de](http://www.arthropod-systematics.de) on 28.ii.2010.

## > Abstract

A jumping cockroach (*Saltoblattella montistabularis*) from Table Mountain, Cape Town, South Africa, is described. The new genus is defined, the characteristics of the species are thoroughly described with particular emphasis on unusual morphological adaptations for jumping. These include dramatic elongation of hind femur and tibia and enlargement of hind femur. The femur ventrally has a longitudinal groove for reception of the tibia during extreme flexure prior to a jump. The euplantulae have unusual surface papillae which may assist landing after a jump. Further modifications from the standard cockroach design probably related to jumping locomotion are hemispherically-protruding compound eyes and a second point of articulation for the first antennal segment. The hook of the male phallomeres is on the left, and the female does not rotate the ootheca prior to deposition. The exact position of the genus within the family Blattellidae is not clear; it is preliminarily placed in Blattellinae. The species and its jumping adaptations are compared with another recently discovered, but extinct jumping ‘cockroach’.

## > Key words

Jumping cockroach, leaproach, Blattodea, Blattellidae, new genus, new species.

## 1. Introduction

The cockroaches have succeeded in populating almost every terrestrial habitat and show diverse morphological, physiological and behavioural adaptations allowing them to survive even under extreme conditions. Many Polyphaginae tolerate the heat and aridity of deserts by burrowing into the sand to depths where soil moisture is high, and are additionally equipped with head modifications allowing the absorption of water from the atmosphere (O'DONNELL 1977). Other cockroaches (Epilamprinae) can swim and even dive in water, and have the last abdominal spiracles elongated to form short tubes, allowing for

gaseous exchange whilst the anterior part of the body is submerged. Some species even use a plastron – a bubble of air held beneath the thorax during diving (TAKAHASHI 1929, in: BELL et al. 2007). True cave-dwelling species (Nocticolidae) show morphological reductions and adaptations typical of trogllobites, such as loss of pigmentation, reduction or loss of eyes and wings, and development of extremely long appendages (ROTH 1991). Cryptocercidae are wood borers, which apart from the necessary morphological adaptations for burrowing in wood have developed a symbiotic relationship with flagellates for the

digestion of cellulose. Assuming that the termites are really the sister group of the Cryptocercidae and therefore nested within Blattodea (for discussion and references see BELL et al. 2007; KLASS & MEIER 2006; INWARD et al. 2007; EGGLETON et al. 2007; WARE et al. 2008; KLASS et al. 2008; ROTH et al. 2009) the development of eusociality in the termites represents the most spectacular case of organismal evolution within the Blattodea.

Successful adaptation to the various habitats mentioned above supposes adaptations of the locomotory apparatus to the different substrates in which the animals live and move. Cryptocercidae inhabiting rotted wood have rather short, stout and heavily sclerotized legs to cope with the strong forces necessary for burrowing. Fossorial Polyphaginae also have short legs, but they are equipped with rather long and strong (tibial) spines broadening the legs to effective shovels. The extremely long legs (and antennae) of Nocticolidae are common troglobitic adaptations for enhanced sensory and locomotory functions. The legs of semi-aquatic Epilamprinae are less modified for specialized locomotion, lacking the leg adaptations of other aquatic insects, such as rows of long bristles that transform legs into effective paddles. It appears that the normal, unmodified leg of cockroaches is already structured as a multifunctional tool allowing a great variety of movements and forms of locomotion. Indeed, most cockroaches are able to move in all directions, horizontally and vertically, on rough as well as on very smooth surfaces. When disturbed, they try to escape by rapid running or by short jumps horizontally or downwards into lower levels of the vegetation. In spite of their unmodified legs they can jump reasonable distances; the small *Blattella germanica* can reach distances of 5 cm in a jump upwards and 4 cm in a horizontal jump (WILLE 1920).

Compared with the jumps of the highly specialized saltatory Orthoptera, the jumping achievements of currently-known cockroaches are quite moderate, and do not include any morphological, physiological or behavioural adaptations that enhance jumping locomotion. But the high evolutionary plasticity of cockroaches and their ancestors was recently revealed with the discovery of a Late-Jurassic stem-dictyopteran adapted to jumping (VRŠANSKÝ 2007). Coincidentally, a living cockroach has now been discovered in South Africa which possesses dramatic modifications resulting in advanced jumping locomotion rivalling that of grasshoppers. The extant jumping cockroach from South Africa is described herein, and its systematic position discussed.

## 2. Materials and methods

**Collecting.** The specimens were collected by a combination of active searching and sweeping with a robust sweep net, killed in alcohol (70%) or in Bouin/Duboscq-Brasil fixative (CLARK 1981) and then stored in alcohol.

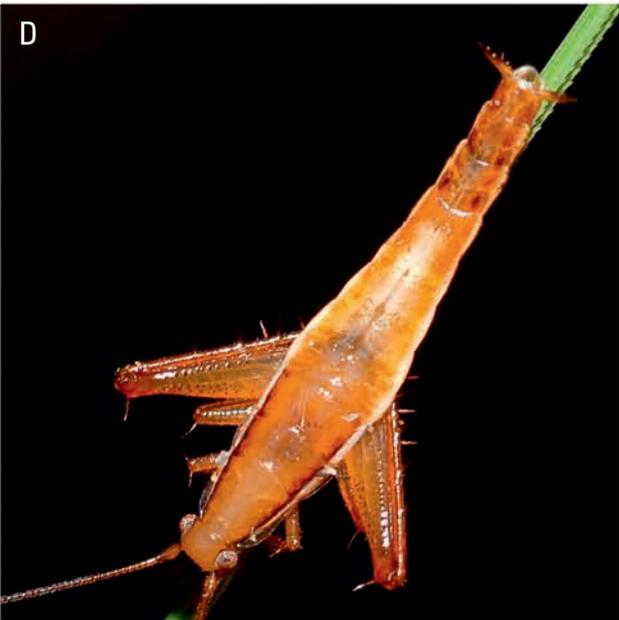
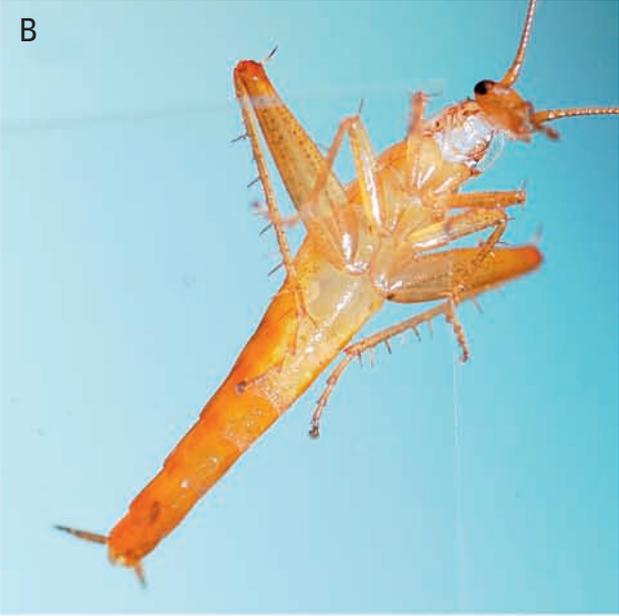
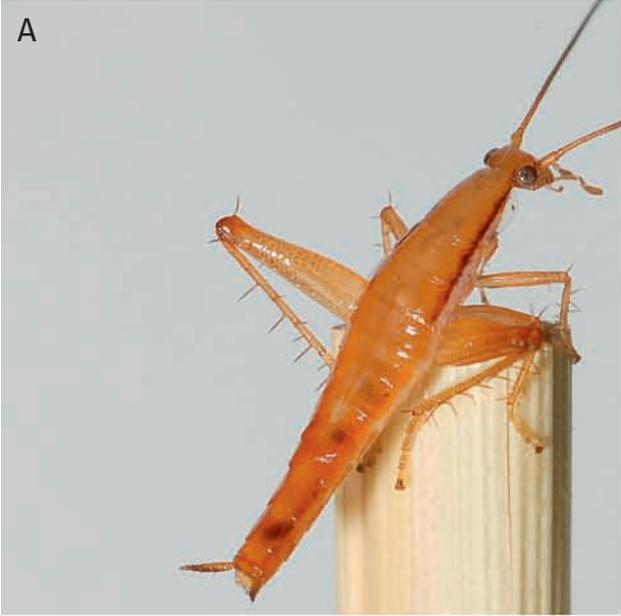
**Microscopical preparations.** For studying and photographing cuticular structures the relevant parts of the body were treated with 10% KOH, and after washing with water transferred to isopropanol, xylol, and finally mounted in Canada Balsam on microscopic slides.

For **images** taken under the compound microscope, the orientation of the depicted structures is with the anterior end on top; dorsal tegumental structures (tergites) are shown in dorsal view, ventral ones (sternites) in ventral view. Deviations from this pattern are mentioned explicitly. The treatment with KOH causes a high transparency of the preparations; therefore, structures from different levels sometimes did shine through. Such instances are explained in the figure legends (Figs. 2H, 4A–C).

**Scanning electron microscopy.** All samples used in scanning electron microscopy were stored in 70% alcohol and subsequently fixed in 5% formalin. Formalin fixed samples were rinsed in a phosphate buffer (pH 7.2), followed by dehydration in an alcohol series before initiation of critical point drying for 2–3 hours using Balzers critical point drier (model CPD 020), sputter coated with gold/palladium alloy to a thickness of 10 angstroms and examined under a LeoS440 analytical SEM.

**Armament of femora and tibiae.** In cockroaches these two podomeres are usually provided with regular patterns of spines, which can be used for systematic and taxonomic considerations. In the armament of the front femur various types are distinguished: Types A, B, C and D (see ROTH 2003) describing the arrangement of spines and spinules along the anteroventral edge of the femur. The distinction of the four types has proved very useful for the characterization of genera and species of the family Blattellidae. In the Blaberidae the arrangement of the spines at the distal end of the femora has turned out to be important; it is described in the following formula:  $n/n + n/n + n/n$ , indicating the respective number of spines ( $n$ ) at the anteroventral/posteroventral edge of

**Fig. 1.** *Saltoblattella montistabularis*, life pictures. **A–D:** Male, in D immediately before the takeoff to a jump, tibia closed up against femur. **E–F:** Female, in F with ootheca. Length of male 9 mm, of female 7 mm.



the femora of the three legs beginning with the front leg.

Both formulae only contain a small part of the potential information available; with the description of new species the neglected information might become important. To allow the economic presentation of more information the following formula for the armament of the femora is proposed:

$[g \cdot (d+p)/(d+p)] [g \cdot (d+p)/(d+p)] [g \cdot (d+p)/(d+p)]$ ,  
 where: [front leg] [mid leg] [hind leg], (anteroventral edge)/(posteroventral edge);  $g$  = number of genicular spines,  $d$  = number of distal spines;  $p$  = number of more proximal spines. When there is variation in the number of spines at a specific position the range should be given (e.g.: 7–9). A row of spinules should be indicated by the letters **sp**. The formulae for the anteroventral edge of the various types of the front femur would be: Type  $A_2$ :  $(2 + p)$ , Type  $B_2$ :  $(2 + sp + p)$ , Type  $C_3$ :  $(3 + sp + 0)$ , Type  $D_1$ :  $(1 + 0)$ . The previously used classification should be maintained, but additionally the full formula for the armament should be given.

For the armament of the tibiae a generalized formula has already been proposed in an earlier paper (BOHN 2006), viz.:  $[a \cdot b \cdot c][a \cdot b \cdot c][a \cdot b \cdot c]$ ;  $a$  = dorsal spines,  $b$  = distal spines,  $c$  = ventral spines. At the dorsal surface of the tibia the spines are usually arranged in three rows, at the ventral surface in two rows. The exceptional occurrence of only two dorsal rows should be mentioned explicitly.

For the future it is recommended that the full formulae of the armament of femora and tibiae be provided in every description of new species even if the armament does not seem to be important for the characterization of that current species.

**Terminology of male and female genitalia** follows that of KLASS (1997, 1998); this terminology includes separate terms for sclerites and for formative elements (such as hooks and apodemes). Regarding male genitalia, synonyms from the terminology of MCKITTRICK (1964) are additionally given (as far as available), and marked by an asterisk; this terminology only includes terms for sclerites.

### 3. Abbreviations

*Morphological terms:* **Pt** paratergite; **S** (coxo)sternite; **S7** (coxo)sternite 7, subgenital plate of female; **S9** (coxo)sternite 9, subgenital plate of male; **T** tergite; **T10** tergite 10, supraanal plate.

*Museums:* **BMNH** British Museum of Natural History, London, UK; **MTD** Museum für Tierkunde, Dresden, FRG; **SAM** South African Museum, Cape Town (Iziko Museums of Cape Town), RSA; **ZSM** Zoologische Staatssammlung München, FRG.

## 4. Descriptions

### 4.1. *Saltoblattella*, gen. nov.

**Diagnosis.** Hind legs modified into long jumping legs resembling those of the Orthoptera, compound eyes hemispherical, only fore wings present forming small lateral lobes, male abdomen elongated, phallomeres of blattellid-blaberid type with fully retractable hook at the left, ootheca not rotated prior to deposition.

**Description.** Head with widely separated hemispherically projecting compound eyes, ocelli absent, antennae longer than body. Pronotum subquadrate, fore wings lobiform, lateral, not longer than mesonotum, hind wings missing. Front femur armament of Type  $E_2$ ; tarsomeres 1–4 with euplantulae; claws symmetrical, shorter than the well developed arolia. Hind legs modified into long jumping legs with a club-shaped femur having a ventral groove for taking up the tibia during full flexion; ventral surface of tibia without spines except for a few distally. Male abdomen long and slender, segments elongated, T7 and T8 even longer than broad, T5 and T6 specialized, subgenital plate (S9) without styli, longitudinal, with a long left and a short right anterior apodeme. Left phallomere with a fully retractable hook (hla with L3 sclerite) and a distally forked endophallus apodeme (lve with parts of sclerite L2). Right phallomere mainly consisting of the cleft sclerite (fused sclerites R1 and R2) with very long arms, sclerite R3 vestigial. Female subgenital plate (S7) entire, with lateral lobes, ootheca not rotated before deposition; genital sclerites with short Pt8,9, basivalvular sclerites of the two sides separated. Cerci in both sexes with 8 annuli, structure of last two atypical.

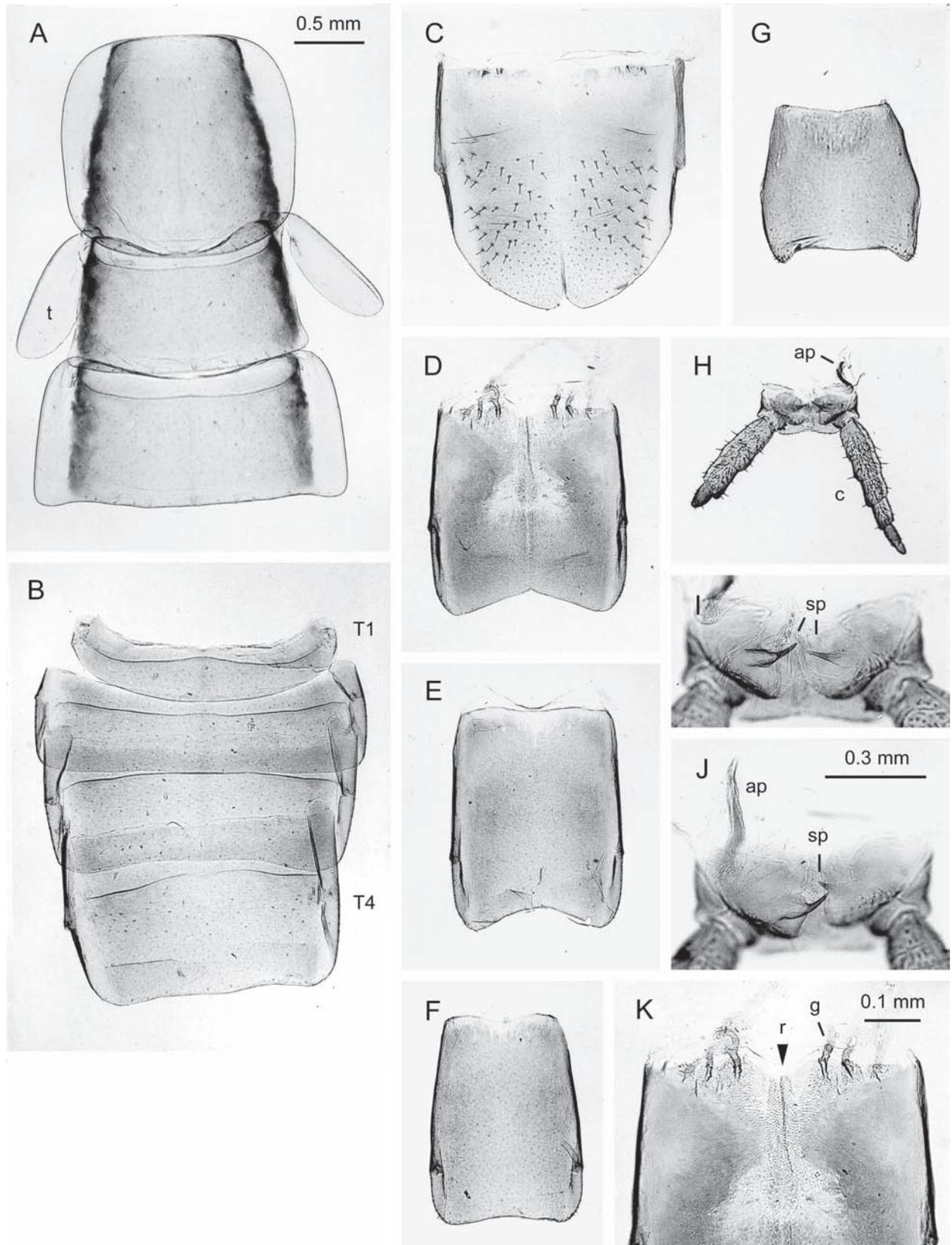
**Etymology.** *Saltoblattella* is the Latin translation of “jumping small cockroach”.

**Type species** of the genus is *Saltoblattella montistabularis*, spec. nov. The genus is monotypic.

### 4.2. *Saltoblattella montistabularis*, spec. nov.

Figs. 1A–F, 2A–K, 3A–F, 4A–K, 5A–I, 6A–C

**Type material.** Holotype, ♂, Republic of South Africa, Western Cape Province, Table Mountain National Park, Silvermine Nature Reserve, 34°04'30"S 18°23'55"E, 460 m, 13.iii.2006, leg. M.D. Picker & J.F. Colville (completely on two slides, Bo 1137). – Paratypes: 1 ♂, 2 ♀♀, same data as holotype; 4 ♂♂,



**Fig. 2.** Segmental structures of the male of *Saltoblattella montistabularis*, holotype (A–I,K), paratype (J). **A:** Thoracic nota, mesonotum with lobiform fore wing (**t**). **B:** Abdominal tergites T1–4. **C:** T5. **D,K:** T6, with the basal parts of six glandular tubes (**g**) and median ridge (**r**). **E:** T7. **F:** T8. **G:** T9. **H:** T10 with cerci (**c**), left cercus abnormal, ventral paraprocts shining through. **I,J:** Paraprocts with spines (**sp**), right paraproct with anterior process (**ap**) (ventral view). Enlargements: Same scale for A–H and for I,J.

4 ♀♀, same data as holotype, but 24.iii.2007 (killed in Bouin/Duboscq-Brasil fixative). – Holotype and paratypes (2 ♂♂, 3 ♀♀) deposited in the collection of the SAM, other paratypes deposited in the BMNH (1 ♂, 1 ♀), the MTD (1 ♂, 1 ♀), and the ZSM (1 ♂, 1 ♀).

**Etymology.** The species name refers to “Mons tabularis”, the old Latin name of Table Mountain near Cape Town where the species has been found; *montistabularis* is the genitive of “Mons tabularis” and therefore indeclinable.

**Distribution.** Currently only known from Table Mountain near Cape Town (RSA, Western Cape Province).

**Description. Size.** Length of body (anterior border of pronotum to posterior border of subgenital plate): ♂ 8–10 mm; ♀ 6.3–7.7 mm; breadth of body (at broadest point): ♂ (metanotum) 2.3 mm; ♀ (abdominal T2) 2.4–2.7 mm; length of pronotum: ♂ 1.4–1.6 mm; ♀ 1.5–1.7 mm; length of wings: 1 mm; length of hind tibia: ♂ 4–5 mm; ♀ 3.8–4.7 mm.

**Head.** Dorsal part of head – above and behind antennal sockets – elongated in dorsoposterior direction, vertex steadily ascending posteriorly, at its highest point passing over to the vertically descending short occiput; occipital foramen, therefore, located quite far dorsally. Compound eyes positioned immediately dorsoposteriorly of the antenna base, in outline roughly circular, only the margin facing the antennal socket straight, almost hemispherically protruding (Fig. 1D,E), ventrally not reaching further than to the middle of the antennal socket. A peripheral ring of unpigmented ommatidia forms a whitish circle around the otherwise dark eye. No ocelli apparent externally. Frons along the dorsal border of the antennal sockets elevated to a low torus. Antennal sockets in addition to the ventral antennophore (= antennifer) with a second supporting sclerite, a narrow bracelet, reaching from the dorsomesal corner of the socket to the dorsal base of the scapus (Fig. 4I); antenna long, surpassing the body considerably. Maxillary palps with penultimate segment usually shorter than the neighbouring ones.

**Thoracic nota** (Fig. 2A). Pronotum unusually long, rounded subquadrate, all borders slightly convex; anteriorly only with a short surmounting margin, head therefore almost uncovered (Fig. 1E). Fore wings tiny lateral lobes, not surpassing the mesonotum and not broader than the transparent lateral margins of pro- and metanotum, separated from its notum down to the base, without any venation. Hind wings completely missing. Lateroposterior corners of mesonotum rounded, of metanotum slightly produced, broadly rounded.

**Legs.** Front leg and mid leg proportioned as in other cockroaches, hind leg developed as jumping leg similar to those of the Orthoptera, with a long, strong, club-shaped femur and a slightly longer, thin tibia, both

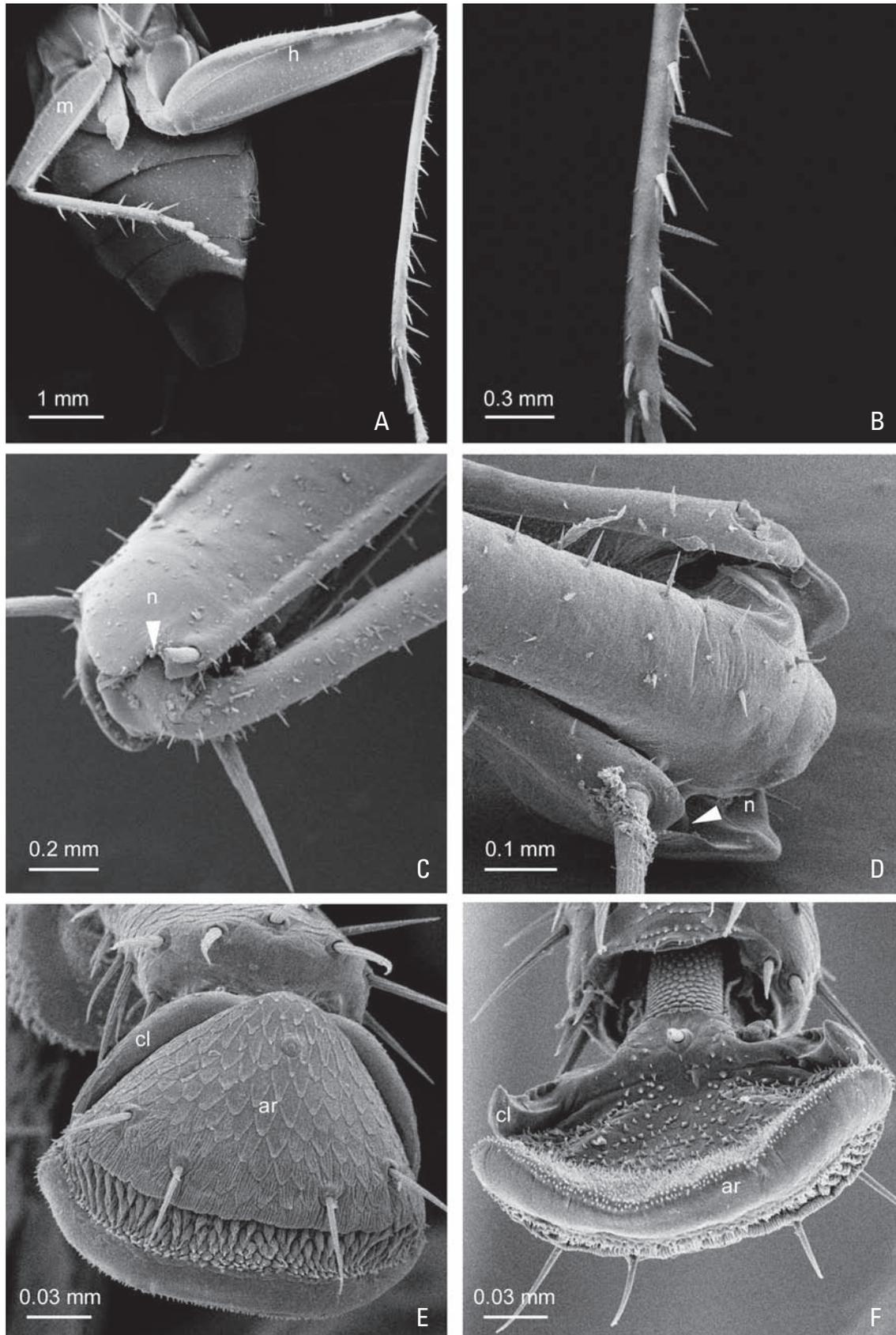
about double the length of the corresponding parts of the mid leg (Fig. 3A). Length of femora and tibiae of the three pairs of legs (anterior to posterior): ♂ (holotype) femora 1.7 / 2.1 / 4.0 mm, tibiae 1.4 / 2.1 / 4.7 mm; ♀ (paratype) femora 1.6 / 2.0 / 3.7 mm, tibiae 1.3 / 2.0 / 4.5 mm. Jumping leg (femur plus tibia) in the male slightly shorter, in the female slightly longer than the body.

Ventral surface of femur of jumping leg deepened to a longitudinal groove taking up the tibia when it is – prior to a jump – maximally flexed and closed up against the femur. Ventral side of tibia, therefore, without spines except 1–2 near the distal end surpassing the femur during flexion (Fig. 3A,B). Distal margin of femur anteriorly and posteriorly with a strongly sclerotized lobe-like distal extension bearing the articulations with the tibia at the ventral edges. Each lobe extends from dorsally near the genicular spine to ventrally shortly above the distal spine of the ventral edge of the femur, where it ends at a wedge-shaped notch in the sclerotization (Fig. 3C,D). The distal shift of the femur-tibia articulations and the mentioned notches presumably serve to make way for the basal parts of the tibia during its movement from extreme flexion to full stretching.

Armament of femora. Front femur at the anteroventral edge with 2 distal spines, followed more proximally by a 3<sup>rd</sup> spine; remaining basal part of the edge with a dense row of small spinules (Fig. 4A). This hitherto unknown type of front femur may be designated as Type E<sub>2</sub>; armament formula of the edge: (2 + 1 + sp). It resembles Type B<sub>2</sub>, having also – apart from the distal spines – fine spinules and 1 or more larger spines, but in reverse arrangement; formula: (2 + sp + x). Further spines on the front femur: posteroventral edge with 1 distal and 1 more proximal spine, no genicular spine. Femora of mid- and hind leg with 1 genicular spine and with 1 distal spine on both edges, proximal part of edges with 0–3 spines. Formula for the armament of the femora of all legs:  $[0 \cdot (2 + 1 + sp) / (1 + 1)] [1 \cdot (1 + 2 - 3) / (1 + 1)] [1 \cdot (1 + 0) / (1 + 1 - 2)]$ .

Armament of tibiae. Tibia spines as usual on the dorsal surface arranged in three, at the ventral surface in two rows. Armament of front and mid leg tibia without remarkable specializations (Fig. 4B,C). Hind leg tibia on the dorsal surface with extremely long spines measuring more than two times the diameter of the tibia, ventral surface only with 1–2 spines near the distal end (Fig. 3B). Formula for the armament of the tibiae:  $[3 \cdot 4 \cdot 3] [5 \cdot 4 \cdot 3] [12 \cdot 5 \cdot 1 - 2]$ .

Tarsi and pretarsi. Basal tarsomere of all legs shorter than remaining tarsomeres together, only covered with normal but relatively strong bristles, no spinules present. Euplantulae present on tarsomeres 1–4 (Fig. 4D,E), in tarsomere 1 of all legs and in tarsomere 2 of the hind leg only covering a distal portion



**Fig. 3.** Leg structures of *Saltoblattella montistabularis*, female, SEM pictures. **A,B:** Right mid leg (**m**) and left hind leg (**h**), notice almost spineless ventral surface of the hind tibia, in **B** in more detail (animal in ventral view, anterior surfaces of the legs exposed). **C,D:** Femur-tibia-joint of the hind leg in anterior (**C**) and ventral view (**D**, with respect to femur), notice the notch (**n**) and – dorsal of it – the distal extension of femur (beyond the spines normally demarcating the distal end of the femur, compare with Fig. 4A–C). **E,F:** Pretarsus and tip of tarsomere 5 of a hind leg in dorsal (**E**) and ventral (**F**) view, **ar** arolium, **cl** claw, with dents visible in **F**.

of segment, in the other tarsomeres larger; euplantulae covered with comparatively large peaked or knob-like processes (Fig. 4D,E), euplantulae of tarsomeres 1 and 2 of the hind leg in the basal part more strongly sclerotized. Claws short and stout, fairly symmetrical, with some dents (Figs. 3F, 4F), otherwise unspecialized; arolium large, surpassing the claws (Figs. 3E,F, 4D,F).

**Male abdomen.** Posterior part of the abdomen elongated and narrowed, almost stick-like. As a consequence, the segments have unusual dimensions: only the basal most segments are broader than long as is the case in other cockroaches and in the female of this species; the relative length increases strongly towards segment 8 and then decreases again (Fig. 2B–H). The dimensions (breadth : length) for the tergites are as follows: T2 (3 : 1), T3 (2 : 1), T4 (1.5 : 1), T5,6 (1 : 1), T7 (0.75 : 1), T8 (0.73 : 1), T9 (1 : 1), T10 (2 : 1). Abdomen in cross section shallowly lens-shaped (basally) to transversely oval (apically), with a lateral keel formed by the margins of T2–8 and the corresponding paratergites. T5 and T6 specialized, with glandular structures.

Tergites. Transversal ridge well developed in T2–4, reduced in T5, completely missing in the tergites following then. **T2–4** with straight or slightly concave posterior border (Fig. 2B). **T5** (Fig. 2C) posteriorly produced to a semicircular lobe with a median notch anteriorly continuing into a short slit, along the longitudinal midline deepened to a groove, on both sides of the groove slightly elevated; surface behind the short remnants of the transversal ridge with dispersed relatively large spatular bristles (Fig. 4J), posteriorly on both sides of notch and slit with tiny but stout bristles. **T6** (Fig. 2D) with obtuse-angularly excised posterior border, anteriorly with a dumb-bell-shaped unsclerotized area which in the longitudinal midline is elevated to a narrow ridge (Fig. 2K); on both sides of the ridge, near the anterior border of the tergite, with the openings of three tubular tergal glands. Glandular tubes of about the length of the segment, basally, near the opening, slightly sclerotized (Fig. 2K); they open from ventrally into a short gutter on the surface of the tergite (Fig. 4K). In normal position T5 is almost completely covering T6; the secretion of the glands presumably first fills the cavity between the two tergites and may finally find its way through the notch and slit into the groove of T5 from where it can be taken up by the female during courtship. The bristles on T5 possibly serve as sensillae signalling to the male the licking movements of the female. **T7–9** with shallowly concave posterior border, otherwise no remarkable structures present (Fig. 2E–G). **T10** (supraanal plate, Fig. 2H) transversely cut shortly behind the insertion of the cerci, posterior border with a slight concavity. Cerci (Fig. 4G) relatively stout, with 8 annuli, last two annuli quite distinct, narrower, palpus-like, with almost

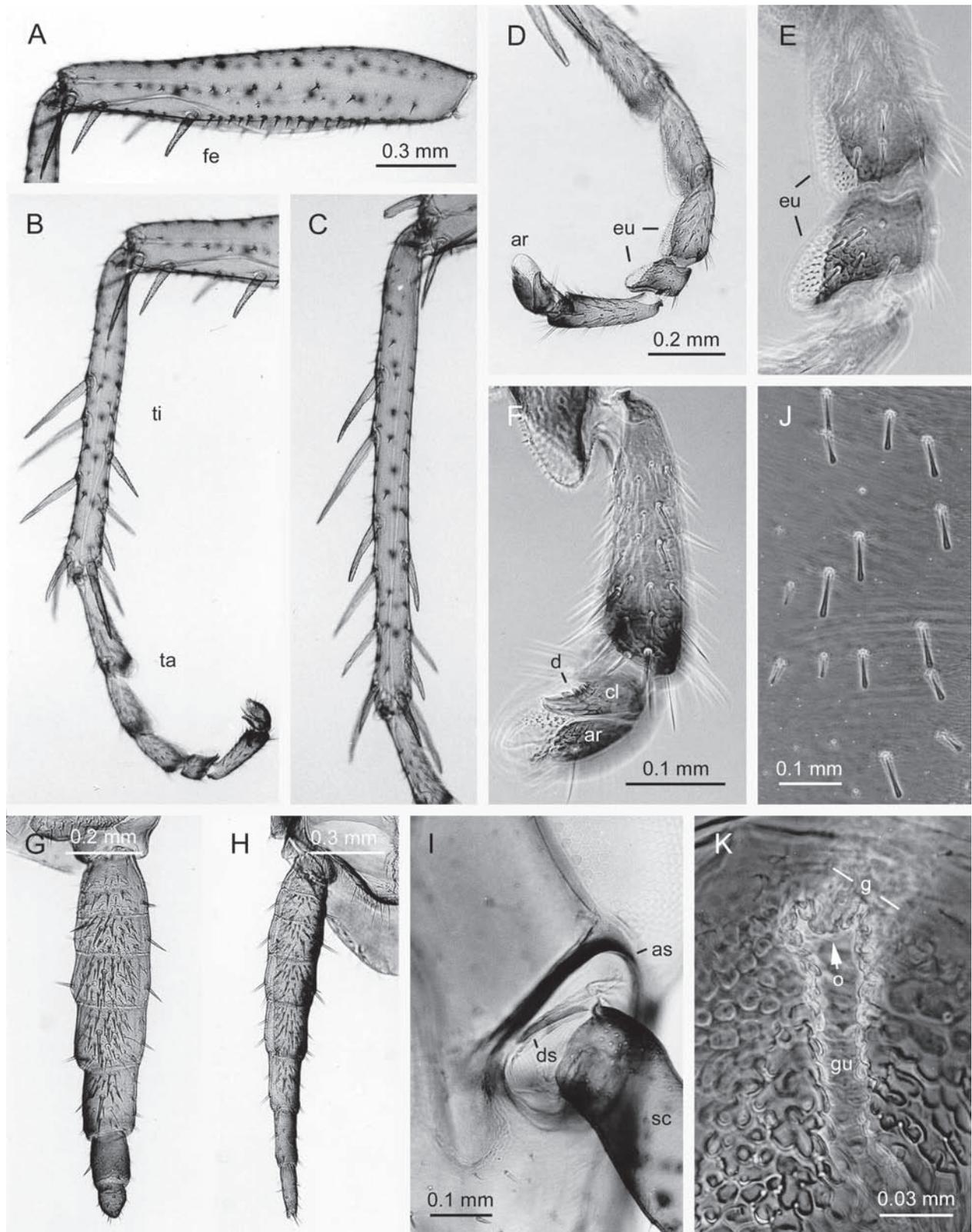
no sensory bristles, last annulus often considerably shorter than the preceding one.

**Sternites. S9** (subgenital plate, Fig. 5A,B) elongated, gutter-shaped, anteriorly with a short right and a long left apodeme, slightly broadening posteriorly, posterior border shallowly rounded bilobed, right lobe slightly larger than left and more densely covered with short bristles. Paraprocts (Fig. 2I,J) each with a slender, slightly curved and anteromesally directed spine, the right usually larger than the left; right paraproct with a narrow anteriorly directed sclerotized process.

Phallomeres (Figs. 5B–E, 6A–C; compare KLASS 1997 for structural details and morphological terms) with normal, uninverted right-left-symmetry, hook at the left, fully retractable. The most conspicuous parts of the phallomeres (Fig. 5B) are the **hook** (hla, Fig. 5D), a weak **sclerite plate** (L4U) partly surrounding the hook (Fig. 5E), further mesal a long and straight, distally forked **endophallic apodeme** (lve, Fig. 5E), at the right a large **cleft sclerite** (cs, Fig. 5C), and anteriorly of the latter a **setose sclerite** (ss, Fig. 5E). In the following the structures of the phallomeres are described in more detail.

Right phallomere with a well developed horseshoe-shaped **cleft sclerite** (Fig. 5B,C); it contains the fused sclerites R1 (forming the lateral arm) and R2 (forming the mesal arm); R1 is not subdivided (R1 + R2 = R1\* of MCKITTRICK 1964). From their point of fusion (upper end of cleft sclerite in Fig. 5C) both the mesal and the lateral arm extend posteriorly and then bend anteroventrally, where they contact the mesal resp. lateral hind margin of sclerite R3 (lower ends in Fig. 5C). R3 is very weak and fairly small (R3\* of MCKITTRICK 1964). In the membrane that descends from the mesal arm R2 of the cleft sclerite to the dorsal parts of the left phallomere (to the dorsal base of the hook) there is a slightly vaulted **lanceolate sclerite** (ls, Fig. 5B,E); it is difficult to interpret, but despite its great distance from R2 it might represent a sclerite R5 (not included in MCKITTRICK's 1964 terminology).

Left phallomere with a long, slender, rod-like **endophallic apodeme** (lve with parts of sclerite L2; Figs. 5B,E, 6). The ejaculatory duct (de) joins the apodeme at ca. 1/4 of its length from internally (Fig. 6A). In the posterior part of apodeme lve (ca. 4/5 from the internal tip) the sclerotization forks into a dorsal arm (sclerite L4N + L2E; separated from the internal parts by an articulation and bearing a tendon txx at its base) and a ventral arm (part of sclerite L2D, continuous with the internal sclerotization of apodeme lve representing the other parts of L2D) (d resp. v, Fig. 5E). The dorsal arm continues posteriorly as a narrow sclerite ribbon and terminally forms a straight, slender process projecting to the outside (vla with a small tendon tve at its dorsal base; Fig. 6B). The ventral arm is slightly curved, and twisted ventrally, where its terminal part is located in



**Fig. 4.** Cuticular structures of *Saltoblattella montistabularis*, holotype (A–F,I,K), paratypes (G,H,J). **A–F:** Leg structures of male, anterior view. **A,B** right front leg. **C** right mid leg. **D,E,F** tarsal structures of left front leg. Abbreviations: **ar** arolium, **cl** claw with dents (**d**), **eu** euplantulae with peaked processes, **fe** femur, **ta** tarsus, **ti** tibia. (The pattern of dark spots on femora and tibiae is less dense than appearing on images A–C, the spots without a central bristle are those from the posterior surface shining through.) **G,H:** Cercus, ventral view, male (G, left cercus), female (H, right cercus). **I:** Left antennal socket (**as**) with dorsal antennophore sclerite (**ds**), **sc** scapus of antenna. **J:** Spatular bristles on T5 of male. **K:** Opening (**o**) of a glandular tube (**g**) into a gutter (**gu**) on T6 of male (same tube as labelled in Fig. 2K with **g**). The tube is out of focus and only visible as a diffuse light band (breadth indicated by the bars); the opening is below the cuticular edge marked by the arrow. Enlargements: Same scale for A–C and for E,F.

a groove; the groove is bordered ventrally by an angular membranous lobe (lo, Fig. 6B,C) (L2D = L2vm\*, and L4N+L2E = L2d\* in MCKITTRICK 1964). A phallosome gland opening in the lve-area was not found. The oval, strongly **setose sclerite** (ss, Figs. 5B,E, 6B) is located far anteriorly in the membrane that runs from the ventral base of the phallosomes to the hind edge of the subgenital plate (and is thus a sclerite in the dorsal wall of the subgenital plate, S9d). Further to the left the ventral base of the phallosomes forms a distinct **tendon** (ate, Figs. 5E, 6A,B). The **hook** (hla, with sclerite L3; L3\* in MCKITTRICK 1964) is located at the (left) hind edge of the phallosome complex, fully retractable, with a short shaft broadened towards the base, tip suddenly narrowed to a curved claw with a strong dent at its base (Fig. 5D); the upper part of the shaft may bear some tubercles, the basal end of the shaft with a conspicuous, slightly sclerotized triangular process (arrow in Fig. 5D). The left wall of the left phallosome – surrounding the retracted hook – bears a rather large dorso-ventrally curved, weak **sclerite plate** (L4U = L2\* in MCKITTRICK 1964: fig. 117); its ventrally located anteromesal tip reaches the base of tendon ate (Figs. 5E, 6A,B).

**Female abdomen.** Relatively slender, but otherwise shape not remarkably different from other cockroaches (Fig. 1E).

Tergites mostly with a straight posterior border and angularly rounded lateroposterior corners. **T9** relatively long (Fig. 5G); **T10** (supraanal plate) posterior lobe behind cerci relatively long, broadly rounded triangular, dorsally along the posterior margin with dispersed bristles (Fig. 5G). Cerci (Fig. 4H) with 8 annuli, gradually narrowing up to the very slender tip, last annulus about as long as the preceding one, last two annuli as in male with almost no sensory bristles. **S7** (subgenital plate, Fig. 5F) in cross section gutter-shaped, longitudinal, basally with two short rounded apodemes, lateral margins curved, converging towards the transversely cut posterior end; no terminal lobes present, but there are lateral lobes of about half the length of the plate, which similarly serve as supports for the ootheca during its formation. The lobes are normally folded mesally but turned outwards (stretched) when an ootheca is produced. Exposed surface of the subgenital plate covered with dispersed bristles.

**Genitalia.** Dorsal complex (Fig. 5G,H): Intercalary sclerite absent; mesal extensions of **Pt8,9** very short, shorter than T9; third valves (gonoplasts) very stout as compared to the other two pairs of valves (gonapophyses 8 and 9); basivalvulae of the two sides separate, narrow and limited to the lateral dorsal wall of the genital chamber, anteriorly angularly converging, anterior part perforated by groups of small pores. One pair of (secondary) spermathecae present, internally undivided; no spermathecal plate present. – Ventral

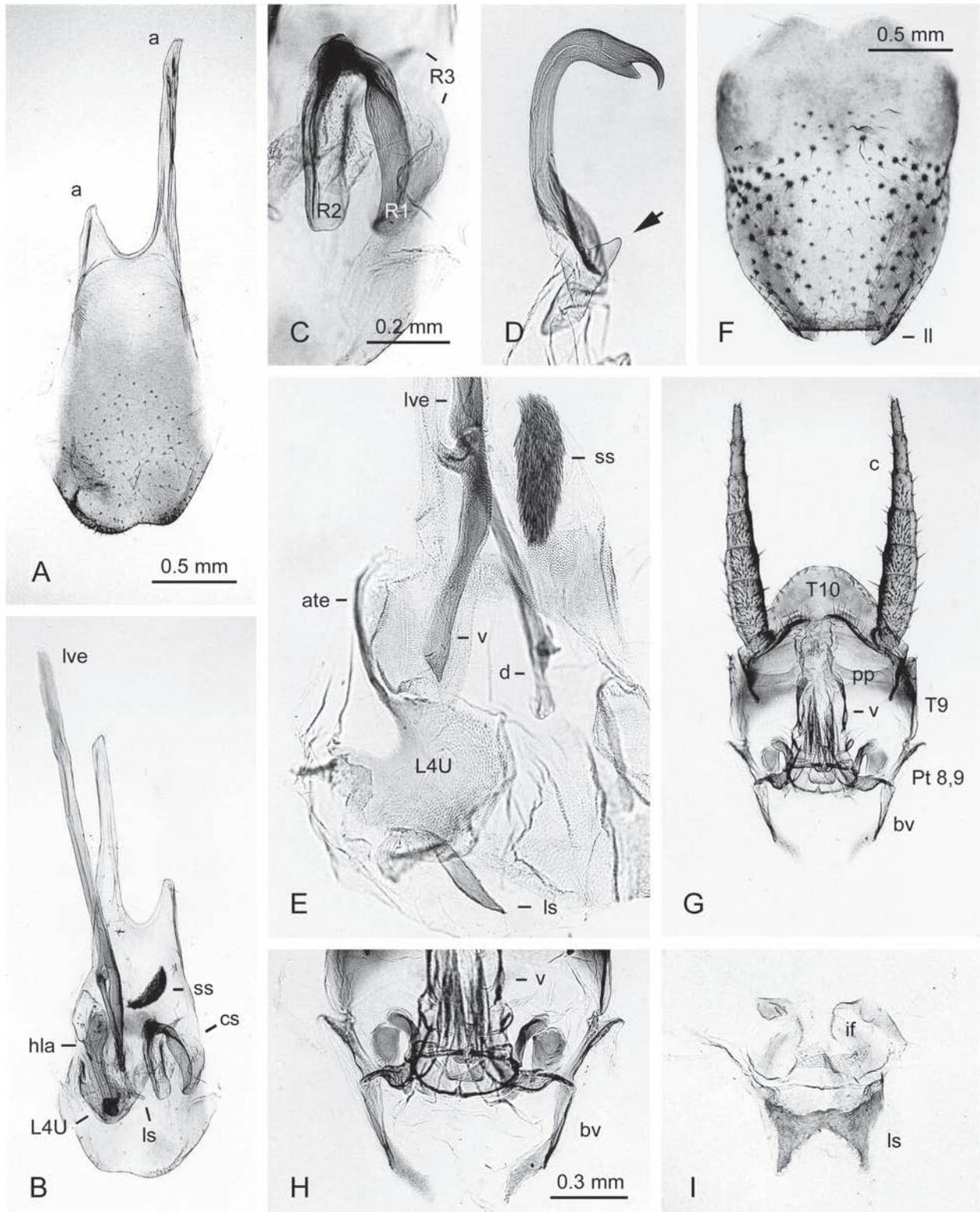
complex (Fig. 5I): Laterosternal shelf relatively small, w-shaped; vestibular sclerite indistinct; intersternal folds well developed.

**Ootheca** (Fig. 1F). Containing about 11 obliquely arranged eggs, surface covered with very fine longitudinal ridges; approximately 4 mm long, 1.7 mm high and 0.7 mm thick. The ootheca is deposited shortly after formation without prior rotation.

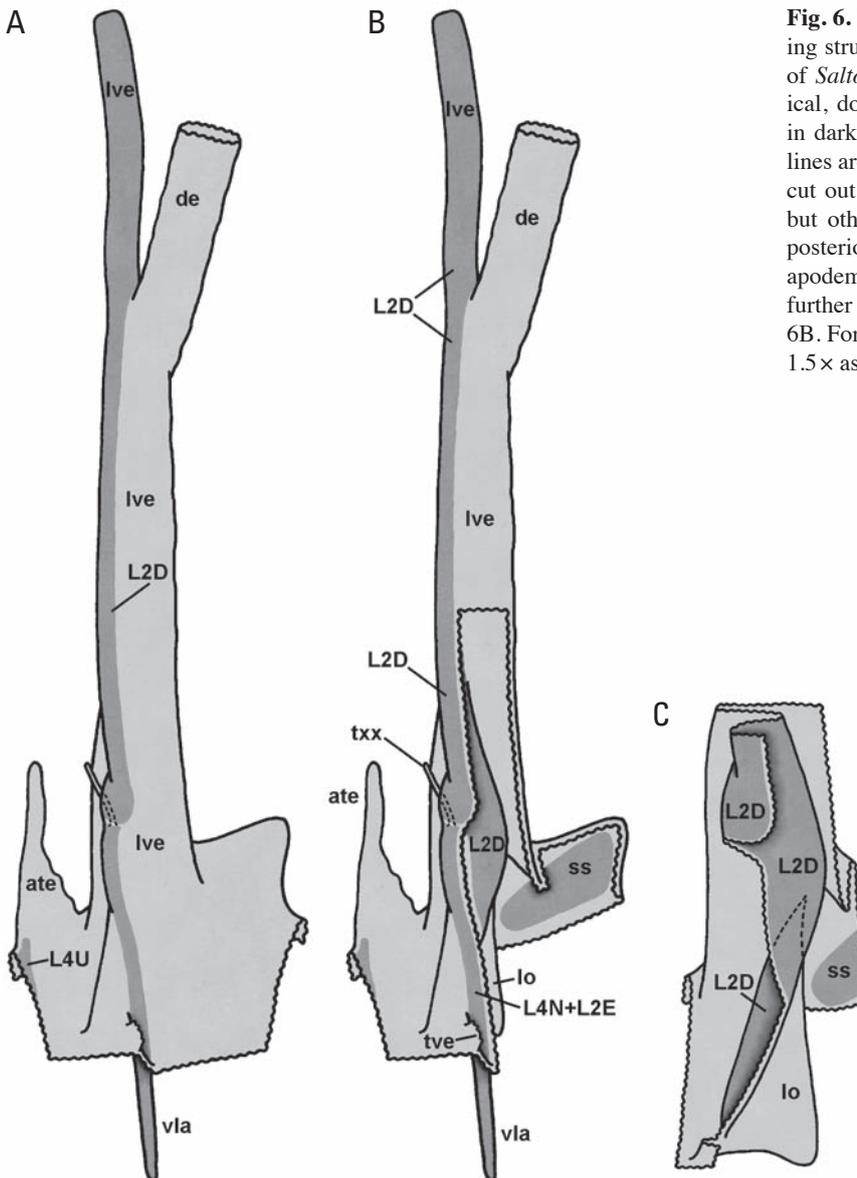
**Colouration in life.** Male (Fig. 1A–D). Similar to female (see below) but more intensely coloured, and with dark markings on the head less distinct. Dorsal side: dark longitudinal band accompanying the white marginal stripe restricted to thorax, thinner, and mesally fading to a brighter reddish-orange; the abdomen is bicoloured, with the anterior half dominated by a median cream-orange area, which in the posterior half is replaced by a brown area broken irregularly by white marbling. Ventrally the colouration is generally light translucent orange, increasing in intensity posteriorly; ventral dark spots much smaller and less distinct than in the female, on the abdomen only present laterally on the five basal sternites.

Female (Fig. 1E,F). Basic colour yellowish. Head yellow, at vertex shading to reddish-orange, without markings except dark linings of the eyes and the antennal sockets, the latter posteriorly continuing into a narrow dark band running along the genae towards the labrum. Antennae yellow, darkening to reddish-orange after flagellomere 11; scapus with dark spots. Tips of maxillary and labial palps dark. Thorax and abdomen dorsally with a white marginal stripe up to T7. On the thorax the white stripe is bounded mesally by a dark brown band which abruptly lightens to yellow; extreme lateral margin of thorax translucent. On the abdomen the marginal stripe is bounded by a broad reddish-orange band, mesally followed by a cream colour; posterior margin of abdominal segments with a broad brown stripe. Ventral side of abdomen as well as femora and tibiae dominated by a pattern of dispersed rounded dark spots with a central bristle; basal sclerites of the legs with darkened borders. Femora translucent, yellow ventrally, shading gradually to orange-brown dorsally, distally and proximally; tibiae and tarsi orange-brown, distal end of last tarsomere dark, femoral and tibial spines dirty yellow, shading to brown distally. Cerci mesally darkened.

**Biology.** Currently leaproaches have only been collected on Table Mountain in the Silvermine Nature Reserve, now part of the Table Mountain National Park. The area experiences winter rainfall and is part of the Fynbos biome, the smallest but biologically one of the richest of the world's biomes (COWLING et al. 1992). The biome supports exceptional levels of floral and faunal endemism and species richness, and



**Fig. 5.** Genital structures of *Saltoblattella montistabularis*, holotype (A), paratypes (B–I). **A–E: Male.** **A, B** subgenital plate, ventral view (A), dorsal view (B) with phallomeres in situ. **C–E** phallomere structures: **C** cleft sclerite with the fused sclerites R1 and R2, notice recurved distal parts; the pointers of R3 mark the position of the hardly visible sclerite. **D** hook hla (arrow points to triangular process at the base of the shaft). **E** part of phallomeres spread out to show some details not visible in B. Abbreviations: **a** anterior apodeme of subgenital plate, **ate** tendon, **cs** cleft sclerite, **d, v** dorsal resp. ventral arm of lve, **hla** hook, **L4U** weakly sclerotized sclerite plate surrounding the hook, **lve** endophallic apodeme, **ls** lanceolate sclerite, **ss** setose sclerite. **F–I: Female.** **F** subgenital plate; **G, H** dorsal complex of genitalia; **I** ventral complex (G, I ventral view, posterior end on top). Abbreviations: **bv** basivalvular sclerites, **if** intersternal folds, **ls** laterosternal shelf, **pp** paraproct, **Pt 8,9** mesal extensions of paratergites 8 and 9, **v** valves. Enlargements: Same scale for A, B, for C, D, E, and for F, G, I.



**Fig. 6.** Endophallic apodeme (Ive) and neighboring structures of male genitalia (left phallomere) of *Saltoblatella montistabularis*, semi-schematic, dorsal views, only cuticle shown; sclerites in dark gray, membranes in light gray, undulate lines are cutting lines through cuticle. **A:** IVE-area cut out from left phallomere (compare Fig. 5B) but otherwise left complete. **B:** Same as A but posterior parts of membranous dorsal wall of IVE-apodeme removed. **C:** Posterior part of IVE with further dorsal parts removed as compared to Fig. 6B. For scale compare with Fig. 5B; 6C enlarged 1.5× as compared to 6A and 6B.

has a strong Gondwanan element (PICKER & SAMWAYS 1996). The locality is situated in mountainous terrain (460 m altitude) in heathland vegetation, classified as Peninsula sandstone fynbos (REBELO et al. 2006). The roaches were only found in areas of dense low vegetation dominated by annual grasses and sedges.

Adults were observed in 2006 and 2007 in late summer from February until the end of April. Although the area was visited at various times of the year, nymphs were never observed. Adult leaproaches are active, diurnal insects, occupying conspicuous positions on grass stalks, where they move between grass culms by prodigious jumps, smaller hops and conventional cockroach scuttling locomotion. The jump mechanics and extent of jumping locomotion in the field are currently under investigation (M. Burrows, M. Picker & J. Colville in prep.). Leaproaches are syntopic with various diurnal, grass-inhabiting Orthoptera. The natural diet is not known, but in cap-

tivity they feed on a range of vegetable matter, as well as on grasshopper frass. Feeding roaches were observed to defend grasshopper frass on which they had been feeding by kicking out at approaching individuals.

## 5. Discussion

### 5.1. Special features of *Saltoblatella*

The new species is characterized by a series of features unique among extant cockroaches. Many of the specializations are apparently jumping adaptations,

reflected in unusual morphology of eyes, antennae, legs and tergite glands.

In most cockroaches the compound eyes are kidney shaped, encompassing the antennal socket at its dorsal and posterior margins; when well-developed they may surpass the socket mesally and ventrally (see drawings in KLASS & EULITZ 2007). In fossorial or troglotic species the eyes are often reduced to small oval structures lying – similarly as in *Saltoblattella* – dorsoposteriorly of the antennal sockets. The hemispherically protruding shape of the *Saltoblattella* eye is unique; though the eye is not very large, the shape and the exposed position at the sides of the head suggest a well developed vision with a large field of view.

The development of a second articulation for the first antennal segment (Fig. 4I) is most likely an adaptation to jumping. The additional point of fixation on the antennal socket would certainly stabilize the long antenna in the airflow developing during jumping.

The legs of cockroaches are generally fairly long and strong and usually allow – apart from walking, running or climbing – at least short leaps from the vegetation downward. Nevertheless, a series of changes was necessary to transform the hind leg into an effective jumping leg: 1) Femur and tibia are strongly elongated allowing a strong leverage effect. 2) The proximal part of the femur is considerably thickened to accommodate the large bundle of tibia extensor muscles. 3) The ventral groove on the femur in combination with a spineless ventral tibia surface allows the full flexion of the tibia; in the flexed position the tibia is locked in the groove and thus stabilized during the first attack of the strong stretching forces. 4) The parts of femur and tibia containing the points of articulation are strengthened. 5) In order to enable full flexion and stretching of the tibia the distal margin of the femur is modified. The distal extensions at the anterior and posterior margins of the femur combined with a distal shift of the points of articulation between femur and tibia make way for the enlarged proximal parts of the tibia. At the dorsal margin, distally of the genicular spine, the extensions enclose a deep membranous recess allowing the accommodation of the enlarged proximal parts of the tibia during full stretching; and the notches at the ventral base of the extensions take up the strong arms bearing the articulation points of the tibia during maximal flexion. Interestingly, similar notches are also present at comparable sites on the femora of the jumping legs of Orthoptera (compare ALBRECHT 1953: figs. 37–38).

The surface structure of the tarsal euplantulae is also unusual. The relatively large domed or knob-like processes provide a rather rough surface which may facilitate the clinging to a similarly rugose surface of

a blade of grass after a jump. In other species studied (ROTH & WILLIS 1952; ARNOLD 1974; BROUSSE-GAURY 1981) the surface of the euplantulae has much finer sculpturing, almost smooth, possibly with some openings of glands producing a wax-like surface film. Euplantulae of this type seem to be better suited for adhesion and movement on rather smooth surfaces as may be found on tree leaves.

The armament of the front femur (Type E<sub>2</sub>) is unlike that of any other cockroach. It contains – though in different arrangement – elements of Type B<sub>2</sub> and may be derived from that type. But though the armament of the femur may yield important features for the characterization of various genera and species, its use for phylogenetic considerations is restricted due to the high incidence of homoplasies.

The pronotum is approximately quadrate in both sexes and thus relatively long. In most cockroaches the pronotum is transverse, but there are species which have a still longer pronotum: species of the genera *Compsagis* Chopard, 1952, *Cyrtotria* Stål, 1871, *Bantua* Shelford, 1908, and *Pilema* Saussure, 1873 (Blaberidae, Perisphaeriinae) boring in wood and soil, and a representative of the cave dwelling Nocticolidae (*Nocticola flabella* Roth, 1991).

The elongate shape of the male's abdomen could be seen as a means of counterbalancing the rotational forces generated during a leap, in convergence with high performance grasshoppers. Although the female has a much broader abdomen, both sexes achieve similar jumping performance (M. Burrows, M. Picker & J. Colville in prep.).

The glandular specializations of tergites 5 and 6 in male *Saltoblattella* are also apparently unique; the glandular secretions are evidently stored between the overlapping parts of the two tergites. In other cockroaches the glands open into variously deep pits where the secretions are stored. One could speculate that the *Saltoblattella* mode of storage avoids a spilling of the secretions during jumping; however, the secretions don't seem to be thinly liquid, and structures found in other cockroaches such as deep pouches with rather small openings may similarly serve that purpose.

The male genitalia of *Saltoblattella* are within the morphological range represented by other higher Blattellidae and Blaberidae (see below). The only unique peculiarity so far known only for *Saltoblattella* is the triangular process on the hook (arrow in Fig. 5D). The reduced condition of sclerite R3, the undivided condition of the R1-arm of the cleft sclerite, the presence of a sclerite ss (Figs. 5E, 6B), and the lack of the phallomere gland and of the styli of the subgenital plate – probably all apomorphies – are also noteworthy but occur in a few other blattellid and blaberid cockroaches as well.

## 5.2. Position in the system of Blattodea

Presently, there are mainly two different conceptions of the system of the Blattodea, that of GRANDCOLAS (1996, 1999) and that of ROTH (2003) which are both modifications of the system developed by MCKITTRICK (1964). We are following the system proposed by ROTH, which comprises six families, viz. Blattidae, Polyphagidae, Cryptocercidae, Nocticolidae, Blattellidae, and Blaberidae. In addition, the phylogenetically isolated lineages Lamproblattidae and Tryonicidae – formerly classified as subfamilies of the Blattidae – have been elevated to family rank by KLASS & MEIER (2006) (see also MURIENNE 2009 for Tryonicidae).

The Blattellidae family contains the majority of genera and species; it is divided into the six subfamilies Anaplectinae, Attaphilinae, Pseudophyllodromiinae (= Plectopterinae), Blattellinae, Nyctiborinae, and Ectobiinae, of which the Pseudophyllodromiinae and Blattellinae are the largest groups. Anaplectinae are generally considered the most basal branch of Blattellidae (MCKITTRICK 1964; GRANDCOLAS 1996; KLASS 1997; KLASS & MEIER 2006). The Pseudophyllodromiinae may be a paraphyletic group constituting several side-branches following the Anaplectinae (KLASS 2001; KLASS & MEIER 2006). Blattellinae, Ectobiinae, and Nyctiborinae likely form a monophyletic group together with the Blaberidae, the Blattellidae thereby being paraphyletic (GRANDCOLAS 1996; KLASS & MEIER 2006; INWARD et al. 2007). The highly specialized Attaphilinae can not yet be placed in this scheme since neither have their genitalia been studied in detail, nor have any genes been sequenced. Unfortunately, the phylogenetic relationships inside the blattellid-blaberid clade have remained poorly analysed, with only few taxa sampled in all previous phylogenetic contributions (except for the usually extensively sampled Blaberidae).

The great number of autapomorphies in *Saltoblattella*, mostly concerning adaptations to jumping, include also the almost complete loss of the wings; thus one important body structure is absent as a source of characters linking *Saltoblattella* with other genera or species of cockroaches. The genitalia, less dependent on environmental constraints, may offer more information about its phylogenetic relationships.

Several characters from the male genitalia as well as the overall morphology of these structures clearly support a placement of *Saltoblattella* in the **clade comprising the Blattellidae and Blaberidae** (compare KLASS 1997: figs. 264–288 and 295–316): 1) There is a long and slender endophallic apodeme (Ive with parts of sclerite L2), which is associated with the ejaculatory duct; 2) the hook (hla with sclerite L3) is located at the hind edge of the phallomeres, and 3) it

can be retracted due to its long membranous base. The presence of paired spermathecae and absence of the plesiomorphic unpaired spermatheca in the female genitalia further suggest a position of *Saltoblattella* in the blattellid-blaberid clade under exclusion of the Anaplectinae (see KLASS & MEIER 2006: character 132; MCKITTRICK 1964: 59). The structure of the female subgenital plate – entire, without terminal lobes or a terminal cleft – and the male subgenital plate – with very long anterior apophyses at least on one side – are in accord with this placement in the blattellid-blaberid clade.

The presence of hook-like structures on the paraprocts of *Saltoblattella* – most likely a synapomorphy of this clade above the level of the **Pseudophyllodromiinae** (H. Bohn, unpublished results) – would also exclude a position in this subfamily. But there is one character which is in conflict with a higher position of *Saltoblattella* in the blattellid-blaberid clade: *Saltoblattella* does not rotate the ootheca prior to its deposition. Placing it there would require the assumption that *Saltoblattella* has either secondarily lost this character or that it represents a side branch shooting off the main clade prior to the development of oothecal rotation.

The latter alternative seems unlikely; the structure of the right phallomere – showing a well developed cleft sclerite combined with a reduction of the other elements – is in a comparable expression only found in ‘higher’ Blattellidae, e.g. Ectobiinae. A loss of the oothecal rotation on the other hand is easily explained. The rotation was certainly an important invention allowing females to carry the ootheca for a longer period of time without being impaired in their moving through narrow spaces. But for a jumping animal carrying the ootheca would be an inconvenient burden. *Saltoblattella* carries the completed ootheca for 1–2 days before it is deposited. In this case the rotation is without any use and, therefore, might be expected to be lost easily during evolution.

The absence of an internal brood sac and the deposition of the ootheca shortly after its completion excludes the placement of *Saltoblattella* in **Blaberidae**. This only leaves the three other subfamilies of the Blattellidae, viz. Blattellinae, Nyctoborinae and Ectobiinae, for placement. (The subfamily **Attaphilinae** with only one genus cannot be included into our considerations for the reasons mentioned above; nevertheless, the highly specialized habit of the species in ant nests and their exclusive distribution in the New World would not suggest a relationship with *Saltoblattella*.)

Among the three subfamilies in question **Nyctiborinae** can also be excluded. The few genera of the subfamily are very uniform in quite a series of external and internal features not found in *Saltoblattella*; moreover, the representatives of Nyctiborinae are quite large animals which only occur in the Neotropics.

The **Blattellinae** are a large heterogeneous and undoubtedly paraphyletic assemblage of genera with mostly unknown mutual relationships. It contains all the genera remaining after the separation of the more derived taxa Nyctiborinae, Ectobiinae and Blaberidae, which are probably all nested somewhere in the Blattellinae. Among the genera of Blattellinae with known genital structures there is none showing a clear affinity to *Saltoblattella*. One feature of its male phallomeres, the posteriorly forked endophallic apodeme (L2), can be found in several genera of the Blattellinae: *Hemithyrsocera* Saussure, 1893 (ROTH 1995), *Symplocodes* Hebard, 1929 (ROTH 1995), *Pseudothyrsocera* Shelford, 1906 (ROTH 1997) and *Burchellia* Rehn, 1933 (H. Bohn, pers. obs.; by GRANDCOLAS 1996 placed in Ectobiinae). But forking seems to be a quite variable feature since it is found only in part of the species of the genera mentioned. Moreover, this forking corresponds with conditions in species of Anaplectinae (*Anaplecta* Burmeister, 1838) and Pseudophyllodromiinae (*Nahublattella* Brujining, 1959) and is certainly plesiomorphic; *Nahublattella* additionally shows the basal articulation of the dorsal branch of the fork, and this articulation has been retained in many higher Blattellidae and Blaberidae (KLASS 1997).

The subfamily **Ectobiinae**, finally, is very small, containing less than ten genera. Nevertheless, the definitions of the characteristic features and the range of appertaining genera differ considerably between authors. According to GRANDCOLAS (1996) Ectobiinae are characterized – apart from some wing features – as having elongated L2D and R3 phallomere sclerites (sclerites L1 and R3v in the terminology of Grandcolas). But this definition is not in agreement with the fact that the name-bearing genus of the subfamily, *Ectobius* Stephens, 1835 (as well as the closely related genus *Phyllodromica* Fieber, 1853), does not have an elongated R3 sclerite; on the contrary, the sclerite is – in comparison to other Blattellidae – strongly reduced in size (see R3 in BOHN 2004: fig. 10A and BOHN 1999: fig. 20M).

PRINCIS (1960, 1971) characterized Ectobiinae as having a large apical triangle in the hind wing curled up spirally at rest. But the applicability of this feature is doubtful. The genera *Burchellia* and *Theganopteryx*, placed by Princis in Ectobiinae, differ from *Ectobius* considerably in the veinal patterns of fore and hind wing (H. Bohn, pers. obs.) which argues for an independent evolution of apical triangle plus curling in these genera. ROTH (2003) has removed *Burchellia* from Ectobiinae because of the deviating genital structures found in this genus. According to the veinal structure of wings, *Theganopteryx* should also be taken out.

With the elimination of these two genera the Ectobiinae form a very homogeneous, presumably mono-

phyletic group consisting of the Palearctic and African genera *Ectobius*, *Phyllodromica* and related genera, and the Australian genera *Choristima* Tepper, 1895, *Ectoneura* Shelford, 1907, and *Stenectoneura* Hebard, 1943. ROTH (1992, 2003) defined this group as having in the male gender a rather long subgenital plate with greatly elongated slender apodemes and one or no style, a greatly elongated genital hook, and a glandular pit with bristles on T7.

Wing structures are not available for the placement of the almost wingless *Saltoblattella*. Of the other characters mentioned only a very small part is present in *Saltoblattella*: it has an elongated subgenital plate with a moderately long anterior apodeme at the left. But the overall elongation of the subgenital plate may be merely a consequence of the elongation of the complete abdomen in the male; remarkably, the females also have an elongated subgenital plate. And a similar unilateral elongation of one of the anterior apodemes of the subgenital plate may be found even in Pseudophyllodromiinae (*Supella* Shelford, 1911).

But there are some more similarities *Saltoblattella* shares with the ectobiine genera *Ectobius* (of which five species are reported from South Africa: PRINCIS 1963) and *Phyllodromica*: The presence of an anterior process at the right paraproct (BOHN 2004), the reduction of sclerite R3 in the right phallomere, the sparse armament of the femora, and a similar structure of pretarsal claws and arolia. However, none of these similarities provide strong arguments for a close relationship: 1) The process at the left paraproct has different positions in *Saltoblattella* and *Ectobius*; it is doubtful that it is homologous in the two taxa. 2) The similarities in the right phallomere appear lightweight in comparison to the great differences in the structure of the left phallomere. 3) Leg structures are often highly variable and susceptible to homoplasies. Thus, a placement of *Saltoblattella* in Ectobiinae does not appear to be sufficiently founded based on the available morphological data.

Notably, however, in a recently completed molecular-based phylogenetic analysis of cockroaches (M. Djernæs and coworkers, submitted), *Saltoblattella* was included and placed as the sister group of *Ectobius*. With regard to the blattellid-blaberid clade, this analysis included 3 genera from Pseudophyllodromiinae, 2 from Blattellinae, 1 from Ectobiinae (*Ectobius*), and 13 from Blaberidae.

The sister group relationship of *Saltoblattella* with *Ectobius* as suggested by the results of the molecular analysis does not justify the inclusion of *Saltoblattella* in Ectobiinae, which in the composition proposed above forms a morphologically homogeneous group. It seems unlikely that *Saltoblattella* is nested within this group. But it might well be that in a future molecular analysis covering more blattelline and ectobiine

genera *Saltoblattella* and the ectobiine genera might be found together with other genera in a larger, presumably monophyletic group. Then a new definition of Ectobiinae should be taken into consideration.

The lack of unequivocal conformities in important characters with any of the known subfamilies of the Blattellidae and the large number of unique characters, not all of which can be considered as adaptations to jumping, might justify the erection of a separate subfamily for *Saltoblattella*. Nevertheless, we hesitate to do so having only one species and genus as representative. We preliminarily place *Saltoblattella* in Blattellinae. The placement in Blattellinae should indicate that it is a representative of the blattellid-blaberid clade above the level of Pseudophyllodromiinae, waiting there together with numerous other genera for a more exact positioning on the phylogenetic tree and in the system of the Blattodea.

The difficulties in unequivocally placing *Saltoblattella* within the system of the Blattodea are, at least partly, a consequence of the incomplete study of many genera of the Blattellidae. In spite of the tremendous work of ROTH (2003), about a quarter of the known genera of Blattellidae still cannot be placed in either Pseudophyllodromiinae or Blattellinae since their genital structures are not sufficiently known. A comprehensive phylogenetic analysis on a larger number of genera using morphological and molecular methods is urgently needed to be able to clarify the phylogeny of the Blattellidae and to resolve the provisional paraphyletic assemblages into monophyletic taxa.

### 5.3. Comparison with the extinct jumping “cockroach”

The recently described Late-Jurassic jumping “cockroach” (*Skok svaba* Vršanský, 2007) is certainly not closely related to *Saltoblattella*. The presence of an external though shortened ovipositor even argues against its placement within the system of the extant Blattodea; it is a member of the large assemblage of mesozoic cockroach-like insects finally giving rise to the modern Dictyoptera including the Blattodea (but see BÉTHOUX & WIELAND 2009 for a possible much earlier origin of Mantodea). VRŠANSKÝ (2007) assumes that the representatives of the Skokidae did not cross the Jurassic/Cretaceous boundary. The jumping adaptations must therefore have been acquired independently in *Skok* and *Saltoblattella*.

*Saltoblattella* seems to be further advanced in its adaptations to jumping compared to *Skok*: 1) The femur of the jumping leg is strongly thickened in its basal half; the corresponding femur in *Skok* is quite ‘nor-

mally’ shaped. 2) The jumping leg (femur plus tibia) is also longer, in females longer than the body; in the female of *Skok* (male unknown) it is shorter than the body. 3) The size difference between the jumping legs and the two anterior pairs of legs is more pronounced; length of mid femur in proportion to the hind femur in *Saltoblattella* is 0.55, in *Skok* 0.78. VRŠANSKÝ (2007) describes the femora of the front legs of *Skok* as being extremely short. But the corresponding structures visible in his fig. 1 presumably only show distal parts of the leg segment since the typical basal narrowing is missing; moreover, it is questionable how a leg with a femur of little more than half of the length of the tibia could function. VRŠANSKÝ (2007) also assumes that *Skok* had “extremely long and free coxae”; in *Saltoblattella* the coxae closely resemble those of typical running cockroaches.

## 6. References

- ALBRECHT, F.O. 1953. The Anatomy of the Migratory Locust. – University of London Press, London, 118 pp.
- ARNOLD, J.W. 1974. Adaptive features on the tarsi of cockroaches (Insecta: Dictyoptera). – International Journal of Insect Morphology and Embryology **3**: 317–334.
- BELL, W.J., L.M. ROTH & C.A. NALEPA 2007. Cockroaches. Ecology, Behavior and Natural History. – The Johns Hopkins University Press, Baltimore, 230 pp.
- BÉTHOUX, O. & F. WIELAND 2009. Evidence for Carboniferous origin of the order Mantodea (Insecta: Dictyoptera) gained from forewing morphology. – Zoological Journal of the Linnean Society **156**: 79–113.
- BOHN, H. 1999. Revision of the *carpetana*-group of *Phyllodromica* Fieber from Spain, Portugal and France (Insecta, Blattaria, Blattellidae, Ectobiinae). – Spixiana, Suppl. **25**: 1–102.
- BOHN, H. 2004. The Blattoptera fauna of Switzerland and the adjacent regions of France, Italy and Austria. I. The species of the *sylvestris*-group of *Ectobius* (Blattellidae, Ectobiinae). – Spixiana **27**: 253–285.
- BROUSSE-GAURY, P. 1981. Typologie et topographie des sensilles sur le tarse des mâles de *Periplaneta americana* L. (Dictyoptères, Blattidae). – Annales des Sciences Naturelles, Zoologie, Paris **3**: 69–94.
- CLARK, G. 1981. Staining Procedures used by the Biological Stains Commission, 4th edn. – Williams & Wilkins, Baltimore, 512 pp.
- COWLING, R.M., P.M. HOLMES & A.G. REBELO 1992. Plant diversity and endemism. Pp. 62–112 in: R.M. COWLING (ed.), The Ecology of Fynbos: Nutrients, Fire and Diversity. – Oxford University Press, Cape Town.
- EGGLETON, P., G. BECCALONI & D. INWARD 2007. Invited reply: Response to Lo et al. – Biology Letters **3**(5): 564–565.
- GRANDCOLAS, P. 1996. The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. – Canadian Journal of Zoology **74**: 508–527.
- GRANDCOLAS, P. 1999. El origen de la diversidad en las Cucarachas: Perspectiva filogenética de su gregarismo, repro-

- ducción, comunicación y ecología. – Boletín de la Sociedad Entomológica Aragonesa **26**: 397–420.
- INWARD, D., G. BECCALONI & P. EGGLETON 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. – *Biology Letters* **3**: 331–335.
- KLASS, K.-D. 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. – *Bonner Zoologische Monographien* **42**: 1–341.
- KLASS, K.-D. 1998. The ovipositor of Dictyoptera (Insecta): homology and ground plan of the main elements. – *Zoologischer Anzeiger* **236**: 69–101.
- KLASS, K.-D. 2001. Morphological evidence on blattarian phylogeny: “phylogenetic histories and stories” (Insecta, Dictyoptera). – *Deutsche Entomologische Zeitschrift* **48**: 223–265.
- KLASS, K.-D. & U. EULITZ 2007. The tentorium and anterior head sulci in Dictyoptera and Mantophasmatodea (Insecta). – *Zoologischer Anzeiger* **246**: 205–234.
- KLASS, K.-D. & R. MEIER 2006. A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. – *Entomologische Abhandlungen* **63**: 3–50.
- KLASS, K.-D., C. NALEPA & N. LO 2008. Wood-feeding cockroaches as models for termite evolution (Insecta: Dictyoptera): *Cryptocercus* vs. *Parasphaeria boleiriana*. – *Molecular Phylogenetics and Evolution* **46**: 809–817.
- McKITTRICK, F.A. 1964. Evolutionary studies of cockroaches. – *Memoirs of the Cornell University Agricultural Experiment Station* **389**: 1–197.
- MURIENNE, J. 2009. Molecular data confirm family status for the *Tryonicus-Lauraesilpha* group (Insecta: Blattodea: Tryonidae). – *Organisms, Diversity & Evolution* **9**: 44–51.
- O'DONNELL, M.J. 1977. Hypopharyngeal bladders and frontal glands: novel structures involved in water vapour absorption in the desert cockroach, *Arenivaga investigata*. – *American Zoologist* **17**: 902.
- PICKER, M.D. & M.J. SAMWAYS 1996. Faunal diversity and endemism of the Cape Peninsula, South Africa – a first assessment. – *Biodiversity and Conservation* **5**: 591–606.
- PRINCIS, K. 1960. Zur Systematik der Blattarien. – *Eos, Revista Española de Entomología* **36**: 427–449.
- PRINCIS, K. 1963. South African Animal Life. Results of the Lund University Expedition in 1950–1951, 9: 9–318. – *Statens Naturvetenskapliga Forskningsrad*, Stockholm.
- PRINCIS, K. 1971. Blattariae: Subordo Epilamproidea, Fam.: Ectobiidae. Pp. 1041–1224 in: M. BEIER (ed.), *Orthopterorum Catalogus*, Pars 14. – Junk, s'Gravenhage.
- REBELO, A.G., C. BOUCHER, N. HELME, L. MUCINA & M.C. RUTHERFORD 2006. Fynbos Biome. – *Strelitzia* **19**: 52–219.
- ROTH, L.M. 1991. A new cave-dwelling cockroach from Western Australia (Blattaria: Nocticolidae). – *Records of the Western Australian Museum* **15**(1): 17–21.
- ROTH, L.M. 1992. The Australian cockroach genus *Choristima* Tepper (Blattaria, Blattellidae: Ectobiinae). – *Entomologica Scandinavica* **23**: 121–151.
- ROTH, L.M. 1995. The cockroach genera *Hemithyrsocera* Saussure and *Symplocodes* Hebard (Dictyoptera: Blattellidae: Blattellinae). – *Invertebrate Taxonomy* **9**: 959–1003.
- ROTH, L.M. 1997. The cockroach genera *Pseudothyrsocera* Shelford, *Haplosymploce* Hanitsch, and *Episymploce* Bey-Bienko (Blattaria: Blattellidae, Blattellinae). – *Tijdschrift voor Entomologie* **140**: 67–110.
- ROTH, L.M. 2003. Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). – *Oriental Insects* **37**: 1–186.
- ROTH, L.M. & E.R. WILLIS 1952. Tarsal structure and climbing ability in cockroaches. – *Journal of Experimental Zoology* **119**: 483–518.
- ROTH, S., B. FROMM, G. GÄDE & R. PREDEL 2009. A proteomic approach for studying insect phylogeny: CAPA peptides of ancient insect taxa (Dictyoptera, Blattoptera) as a test case. – *BMC Evolutionary Biology* **9**: 50, doi:10.1186/1471-2148-9-50.
- VRŠANSKÝ, P. 2007. Jumping cockroaches (Blattaria, Skokidae fam. n.) from the late Jurassic of Karatau in Kazakhstan. – *Biologia, Bratislava* **62**(5): 588–592.
- WARE, J., J. LITMAN, K.-D. KLASS & L. SPEARMAN 2008. Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. – *Systematic Entomology* **33**: 429–450.
- WILLE, J. 1920. Biologie und Bekämpfung der deutschen Schabe (*Phyllodromia germanica* L.). – *Monographien zur angewandten Entomologie* **5**: 1–140.