The external morphology of eggs of three Rhopalidae species (Hemiptera: Heteroptera) with a review of the eggs of this family

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Abstract. The external morphology of eggs and manner of oviposition of three rhopalid species, *Brachycarenus tigrinus* (Schilling, 1829), *Chorosoma schillingi* (Schilling, 1829) and *Rhopalus (Aeschyntelus) maculatus* (Fieber, 1837) are described. The eggs were studied using Scanning Electron Microscopy (SEM), and the results complete previous observations. The emphasis of the study is on the characteristics of eggs and details of oviposition in representatives of the family Rhopalidae. The chorionic origin of attachment stalk was confirmed only in the Chorosomatini. A completely smooth egg chorion was recognized in *R*. (*A*.) *maculatus*, as a unique condition within at least the Pentatomomorpha.

Key words. Rhopalidae, Rhopalini, Chorosomatini, *Brachycarenus tigrinus, Chorosoma schillingi, Rhopalus (Aeschyntelus) maculatus*, egg structure, micropylar processes, chorion, attachment stalk, oviposition

Introduction

Heteroptera eggs have a stable shape due to a sclerotized chorion. Egg morphology is helpful for taxonomic and phylogenetic purposes. The morphology of heteropteran eggs varies distinctly among taxa; for details see two monographs: SOUTHWOOD (1956) and COB-BEN (1968). Both authors mentioned that the eggs of the coreoid family Rhopalidae have a specific morphological pattern (e.g. two micropylar processes). COBBEN (1968) not only compared the morphology of heteropteran eggs but made phylogenetic inferences from their important characters.

The eggs of several rhopalid genera and species have been decribed and/or illustrated. However, the descriptions are mostly brief with simplified illustrations such as line drawings (e.g. PANIZZI et al. (2005): *Jadera choprai* Göllner-Scheiding, 1979; PASKEWITZ & MCPHERSON (1983): Arhyssus lateralis Say, 1825; WHEELER (1977): Niesthrea louisianica Sailer, 1961 and others). Representative papers pertaining to eggs of Rhopalidae are listed in Table 1.

MICHALK (1935) used *Chorosoma schillingi* (Schilling, 1829) as a type for eggs laid horizontally with an attachment stalk ('columniert'). PUTSHKOVA (1955, 1957) interpreted the rhopalid eggs as a subgroup within the Coreoidea. Descriptions of rhopalid eggs are also available in defined areas such as Great Britain (BUTLER 1923), Ukraine (PUTSHKOV 1962, 1986) and France (MOULET 1995).

Recently, WHEELER & HOEBEKE (1988) and CANDAN et al. (2004) provided more detailed information on eggs of *Brachycarenus tigrinus* (Schilling, 1829) (as *Rhopalus (Brachycarenus) tigrinus*; our nomenclature used according to Dolling (2006)) (Rhopalinae: Rhopalini), and *Maccevethus corsicus corsicus* Signoret, 1862 (as *Maccevethus lutheri* Wagner, 1953) (Rhopalinae: Maccevethini), respectively, based on scanning electron microscopy studies.

The present paper presents a detailed study of external morphology, oviposition and hatching of eggs of three species of the subfamily Rhopalinae, *Rhopalus (Aeschyntelus) maculatus* (Fieber, 1837) and *Brachycarenus tigrinus* (both Rhopalini), and *Chorosoma schillingi* (Chorosomatini). Using comparison of previously published data on rhopalid egg morphology, we review the characteristics of the higher taxa and their relationships.

Material and methods

Material examined. Females of all species studied were collected in the Czech Republic during 1994–1996 from the following localities: *Rhopalus (Aeschyntelus) maculatus*: Southern Bohemia, Veselí nad Lužnicí environment (map grids 6853, 6854, according to PRUNER & MíkA (1996)) and Southern Moravia, Vranov nad Dyjí environment (7160); *Brachycarenus tigrinus*: Southern Moravia, Havraníky environment (7162); and *Chorosoma schillingi*: Southern Moravia, Havraníky environment (7162). Females were reared in the laboratory under common garden conditions on their food plants (see Table 2) until they oviposited. The eggs were fixed in 75% ethanol.

Methods. A stereomicroscope Olympus SD 30 with an ocular grid was used to take measurements. The length, width and height were measured in eggs of *Chorosoma schillingi* (tribe Chorosomatini), and *Rhopalus* (*Aeschyntelus*) maculatus (tribe Rhopalini). Ten eggs of each species were measured (Table 3).

The material for SEM was prepared by standard methods, including coating with a sputter apparatus Bal-Tec SCD 050. Scanning electron microscope JEOL 6300 was used.

Terminology. PUTSHKOVA (1957) and COBBEN (1968) used a topographical terminology of eggs based on the orientation of the contained embryo. The egg side/surface/wall, which corresponds with dorsum of the embryo, is dorsal. COBBEN (1968) preferred the term 'aft' for the side most closely associated with the substrate rather than the morphological term dorsal. The dorsal surface of the egg is then oriented ventrally during oviposition, i.e. attached to the substrate. CANDAN et al. (2004) also correctly described the orientation of the egg sides.

In our view, the following authors failed to describe the egg sides correctly, in that they used the orientation of the egg after oviposition with the ventral side of the egg attached to the substrate: SOUTHWOOD (1956), WHEELER (1977), PASKEWITZ & MCPHERSON (1983), WHEELER

Taxon studied	Papers				
Serinethinae					
Boisea trivittata (Say,1825)	YODER & ROBINSON (1990), SCHAEFER & KOTULSKI (2000), GRIMNES et al. (2003)				
Jadera choprai Göllner-Scheiding, 1979	PANIZZI et al. (2005)				
Leptocoris augur (Fieber, 1781)	MALHOTRA (1958, as Serinetha augur), SCHAEFER & KOTULSI (2000)				
Leptocoris mitellata Bergroth, 1916	Kumar (1966)				
Leptocoris tagalica Burmeister, 1834	Kumar (1966)				
Rhopalinae: Chorosomatini					
Agraphopus viridis (Jakovlev, 1872)	PUTSHKOVA (1957; as Leptoceraea viridis), PUTSHKOV (1962)				
Chorosoma schillingi (Schilling, 1829)	REUTER (1910), BUTLER (1912, 1923), MICHALK (1935), SOUTH- WOOD (1956), KIRITSHENKO (1957), PUTSHKOVA (1957), SOUTHWOOD & LESTON (1959), COBBEN (1968), PUTSHKOV (1962, 1986), MOULET (1995)				
Myrmus miriformis miriformis (Fallén, 1807)	BUTLER (1912, 1923), MICHALK (1935), SOUTHWOOD (1956), KIRI- TSHENKO (1957), PUTSHKOVA (1957), PUTSHKOV (1962, 1986)				
Rhopalinae: Harmostini					
Harmostes fraterculus (Say, 1832)	Wheeler & Miller (1983)				
Rhopalinae: Maccevethini					
Maccevethus corsicus corsicus Signoret, 1862	Ритsнкоva (1957, as <i>M. lineola</i>), Ритsнкоv (1962, as <i>M. lineola</i> ; 1986), Candan et al. (2004, as <i>M. lutheri</i>)				
Maccevethus errans (Fabricius, 1794)	Moulet (1995)				
Stictopleurus abutilon (Rossi, 1790)	Ритянкоv (1962, 1986)				
Stictopleurus crassicornis (Linnaeus, 1758)	Ритянкоv (1962, 1986)				
Stictopleurus punctatonervosus (Goeze, 1778)	Putshkov (1962, 1986), Moulet (1995)				
Stictopleurus sp.	Putshkova (1955, 1957)				
Rhopalinae: Niesthreini					
Arhyssus lateralis (Say, 1825)	HAMBLETON (1909, as <i>Corizus lateralis</i>), READIO (1928, as <i>Corizus lateralis</i>), PASKEWITZ & MCPHERSON (1983)				
Niesthrea louisianica Sailer, 1961	Wheeler (1977)				
Niesthrea sidae (Fabricius, 1794)	READIO (1928, as Corizus sidae)				
Rhopalinae: Rhopalini					
Brachycarenus tigrinus (Schilling, 1829)	Ритянкоva (1957), Ритянкоv (1962, 1986), Wheeler & Hoebeke (1988), Moulet (1995)				
Corizus hyoscyami (Linnaeus, 1758)	Butler (1923), Zwaluwenburg (1944), Schwoerbel (1956), Putshkova (1957), Putshkov (1962, 1986), Moulet (1995)				
Liorhyssus hyalinus (Fabricius, 1794)	KIRKALDY (1907, as <i>Rhopalus hyalinus</i>), READIO (1928, as <i>Corizus hyalinus</i>), PUTSHKOVA (1957), PUTSHKOV (1962, 1986), ATALAY (1978), MOULET (1995), MINEO (2004, 2005), HRADIL et al. (2007)				
Rhopalus distinctus (Signoret, 1859)	Putshkova (1957), Putshkov (1962, 1986)				
Rhopalus parumpunctatus (Schilling, 1817)	Michalk (1935), Stroyan (1954), Kiritshenko (1957), Putshkova (1957), Putshkov (1962, 1986), Moulet (1995)				
Rhopalus subrufus (Gmelin, 1788)	Putshkov (1962, 1986), Moulet (1995)				
Rhopalus sp.	Ритянкоvа (1955)				

Table 1. Literature references containing data on rhopalid eggs

Table 2. Food plants of *Chorosoma schillingi* (Schilling, 1829) and *Rhopalus* (*Aeschynteles*) maculatus (Fieber, 1837)

Chorosoma schillingi		Rhopalus (A.) maculatus			
Poaceae	Elytrigia repens (L.) Nevski	Asteraceae	Cirsium palustre (L.) Scop.		
	Calamagrostis epigeios (L.) Roth	Rosaceae	Comarum palustre L.		
	Koeleria glauca (Schrad.) Dc.	Hypericaceae	Hypericum pulchrum L.		
	Phleum pratense L. (new food plant)				
	Poa sp.				

& HOEBEKE (1988) and MOULET (1995). This situation may cause problems or inaccuracies when egg descriptions by different authors are compared.

The specific columnar element on the dorsal side of the egg fastening it to the substrate is characteristic for Coreidae and Rhopalidae (SOUTHWOOD 1956). This structure is at least in *Ch. schillingi* (SOUTHWOOD 1956, COBBEN 1968) part of the chorion. Several other terms have been used for this structure, e.g. pedicel, stalk, attachment stalk, 'leg/leglet' (literal translation from Russian).

We used a terminology for eggs based on the position of the embryo, i.e. dorsal is the side oriented towards the substrate. For the special chorionic structure by which the egg is attached to the substrate we have chosen the term attachment stalk. The other terms used hereinafter are defined by SOUTHWOOD (1956) and COBBEN (1968).

Results

Description of the eggs

Chorosoma schillingi (Schilling, 1829)

(Figs. 1-10, Table 3)

Egg is oval, roughly bean-shaped. Dorsal side is convex, differing from all other species studied, with attachment stalk situated medially, in longitudinal axis almost centrally, only slightly closer to posterior egg pole than to anterior pole. Lateral sides are only slightly sunken/concave longitudinally, each slanting toward ventral side. Ventral side is narrower than dorsal, merging gradually into lateral sides, without any conspicuous structures, as e.g. longitudinal ribs in *Rhopalus maculatus*.

In hatching, the larva forces off the pseudoperculum at anterior egg pole. Pseudoperculum is rounded, almost circular, flattened and distinctly separated by paler ring with slightly indicated ridge of different structure from surrounding chorion. Convex chorionic elevations in shape of elongated rhomboids form structure of this ridge.

Chorion is dull, with tetragonal, approximately rhomboidal convex elevations emarginated by low ridges, and with small convex central plate in each tetragon. Structure of pseudoperculum is slightly different from that of surrounding chorion; ridges demarcating elevations are less distinct.

Chorosomatini: Chorosoma schillingi				Rhopalini: Rhopalus (Aeschynteles) maculatus					
Egg	length	width	height	height/length	Egg	length	width	height	height/length
				ratio					ratio
1	1.28	0.56	0.65	0.51	1	0.97	0.49	0.54	0.56
2	1.33	0.54	0.60	0.45	2	0.97	0.48	0.53	0.55
3	1.26	0.51	0.66	0.52	3	0.99	0.49	0.54	0.55
4	1.20	0.53	0.63	0.53	4	1.04	0.49	0.58	0.56
5	1.20	0.54	0.66	0.55	5	1.02	0.46	0.51	0.50
6	1.24	0.60	0.66	0.53	6	1.00	0.49	0.49	0.49
7	1.14	0.60	0.60	0.53	7	1.02	0.53	0.51	0.50
8	1.21	0.56	0.63	0.52	8	1.05	0.51	0.53	0.50
9	1.21	0.58	0.60	0.50	9	1.07	0.51	0.51	0.48
10	1.24	0.60	0.66	0.53	10	0.97	0.51	0.51	0.53
min.	1.14	0.51	0.60	0.45	min.	0.97	0.48	0.49	0.48
max.	1.33	0.60	0.66	0.55	max.	1.07	0.53	0.58	0.56
mean	1.23	0.56	0.64	0.52	mean	1.01	0.50	0.53	0.52

Table 3. Size of the eggs of *Chorosoma schillingi* (Schilling, 1829) and *Rhopalus* (Aeschynteles) maculatus (Fieber, 1837)

Two micropylar processes are in longitudinal egg axis, one is on pseudoperculum close to the anterior pole of egg, the other on dorsal side close to pseudoperculum and anterior egg pole. Micropyle is distinct, larger than in Rhopalini, protruding from egg outline. It has a more complicated, S shape in lateral view, with short stem and broaden apex with single opening directed roughly anteriad.

Attachment stalk is developed as distinct chorionic structure roughly in center of dorsal egg side. It is about the same size as micropyle, cylindrical with slightly broadened apex, and surface smooth.

Egg is brown after oviposition, darkening to brown to blackish.

Measurements (in mm): length 1.23 (1.14–1.33), width 0.56 (0.51–0.60).

Brachycarenus tigrinus (Schilling, 1829)

(Figs. 11-16)

Egg is elongated, rounded, more slender than eggs of *Ch. schillingi* and *R. maculatus*. Dorsal side is slightly convex, wide, without attachment stalk. Lateral sides are only slightly sunken longitudinally. Ventral side is narrower than dorsal, merging continuously into lateral sides without any special structures, such as longitudinal ribs.

In hatching, the larva forces off the pseudoperculum at anterior egg pole. Pseudoperculum is almost circular, slightly flattened and separated from surrounding chorion by pale low ridge of different structure. Chorion of this ridge with only fine tubercles to almost smooth.

Chorion is dull, with distinct low rounded tubercles in regular arrangement, surface between tubercles smooth. Structure of pseudoperculum identical with egg body.



Figs. 1–8. Eggs of *Chorosoma schillingi* (Schilling, 1829). 1 – whole egg, ventral view; 2 – whole egg, lateral view; 3 – anterior pole of egg, lateral view; 4 – anterior pole of egg, ventral view; 5 – empty egg with separated pseudo-perculum, ventral view; 6 – detail of chorion surface pattern, pseudoperculum; 7 – detail of chorion surface pattern, egg body; 8 – detail of adhesive stalk on dorsal side, lateral view. Scale = 100 μ m for Figs. 1–5; 10 μ m for Figs. 6–8. Letterings: c – cap; m1, m2 – micropylar processes; p – pseudoperculum; r – ridge separating pseudoperculum from surrounding chorion; s – attachment stalk.



Figs. 9–10. Eggs of *Chorosoma schillingi* (Schilling, 1829). 9 – apex of micropylar process, most exposed view; 10 - cuticular cap of hatched larva attached to empty egg, with egg burster, most exposed view. Scale = $100 \mu m$ for Fig. 10; 10 μm for Fig. 9. Letterings: b – egg burster; o – opening of micropylar process.

Two micropylar processes are in longitudinal egg axis, one is on pseudoperculum close to the anterior egg pole, the other on dorsal side close to pseudoperculum and anterior egg pole. Micropyle is shaped as simple bent conical channel with single apical opening, directed dorsoposteriad or ventroposteriad. Entire micropylar process is bent posteriorly and pressed to chorion, thus appearing as a small rounded tubercle.

Egg is green after oviposition, becoming dark green-brown.

Measurements (in mm): length 1.11 (1.10–1.14), width 0.37 (0.35–0.39).

Rhopalus (Aeschyntelus) maculatus (Fieber, 1837) (Figs.17–22, Table 3)

Egg is oblong, bean-shaped. Dorsal side is slightly convex, relatively wide, without attachment stalk. Lateral sides are slightly sunken longitudinally. Ventral side is narrower than dorsal, narrowing towards middle, with two dark longitudinal, strongly sclerotized ribs at narrowest part stiffening egg surface.

In hatching, the larva forces off the oval pseudoperculum at anterior egg pole. Pseudoperculum is imperceptible without any border with surrounding chorion.

Chorion is glossy, smooth, including pseudoperculum.

Two micropylar processes are in longitudinal axis, one is located on pseudoperculum close to the anterior pole of egg, the other on dorsal side close to pseudoperculum and anterior pole. Micropyle is shaped as simple bent conical channel slightly narrowing toward its apex, with single apical opening directed dorsoposteriad or ventroposteriad. Entire micropylar process is bent posteriorly and pressed to chorion, thus appearing as a small rounded tubercle.

Egg is goldish after oviposition, becoming yellow-brown to brown, due to embryo showing through.

Measurements (in mm): length 1.01 (0.97–1.07), width 0.50 (0.48–0.53).

Oviposition

Chorosoma schillingi (Schilling, 1829)

Eggs are deposited in exposed batches on stalks and spikes of food plants, which are restricted to the Poaceae (see Table 2). There can be 6 to 20 eggs in a batch. Eggs are deposited with the dorsal sides toward plant, parallel to the substrate, glued by an adhesive secretion of female, which is deposited in an irregular film layer on the apices of the attachment stalks and hardens shortly after oviposition upon contact with the air.

Brachycarenus tigrinus (Schilling, 1829)

Eggs are deposited singly, exposed on leaves of food plants (e.g. *Capsella bursa-pastoris* (L.) Medik., *Lepidium ruderale* (L.), both Brassicaceae). Eggs are laid with the dorsal side toward leaf, parallel to substrate, glued by female adhesive secretion located centrally on dorsal side, with the secretion stiffening soon after oviposition. No special chorionic structure for attachment was recognized.

Rhopalus (A.) maculatus (Fieber, 1837)

Eggs are deposited singly, exposed on leaves and flowers of food plants, mostly *Comarum palustre* L. (Rosaceae) (food plants are listed in Table 2). Eggs are laid with the dorsal side toward leaf, parallel to substrate, glued by the female's adhesive secretion, which stiffens shortly after oviposition into an irregularly shaped area. Most eggs were glued directly by their surface, approximately centrally on dorsal side, to the leaf/flower. However, in about 12 % of the eggs the solid secretion formed a columnar structure that resembled the chorionic stalk of *Ch. schillingi*. This structure, in the form of a 'leglet', elevates the egg above the surface. It is surely not of chorionic origin because it can be separated from the chorion, using only slight force, without damaging the egg.

Hatching

The hatching larva opens the egg at the anterior pole. The egg chorion is forced off at eclosion in the form of a pseudoperculum. The pseudoperculum is separated from the egg body around its margin, starting from the most exposed apex toward the ventral side. All species studied have a special structure, the egg burster, that is a median sclerotized area of the vertex of the embryonic cuticle. The rest of the embryonic cuticle remains attached to the empty egg shell after the larva hatches. The strongly sclerotized head part is called a cap, with the egg burster on it consisting of transverse, elevated ridges. The embryonic cap and egg burster were studied in detail only in *Ch. schillingi* and *R. maculatus*.

The cap is convex in both species, laterally elongated; the egg burster is located in its longitudinal axis closer to the anterior than the posterior margin, at the highest point of the cap.

Rhopalus maculatus. Cap is roughly pentagonal, egg burster is formed by three elevated, strongly sclerotized ridges, two ridges running laterally and one ridge dorsally.



Figs. 11–16. Eggs of *Brachycarenus tigrinus* (Schilling, 1829). 11 – empty egg with separated pseudoperculum, ventral view; 12 – empty egg with separated pseudoperculum, lateral view; 13 – detail of boundary-line between egg body and pseudoperculum, anterolateral view; 14 – detail of micropylar process, most exposed view; 15 – anterior pole of egg with one micropylar process visible, dorsal view; 16 – detail of chorion pattern with rounded elevated tubercles. Scale = 100 μ m for Figs. 11, 12, 15; 50 μ m for Fig. 13; 10 μ m for Figs 14, 16. Letterings: m1, m2 – micropylar processes; p – pseudoperculum.



Figs. 17–22. Eggs of *Rhopalus (Aeschyntelus) maculatus* (Fieber, 1837). 17 – whole egg, ventral view; 18 – whole egg, lateral view; 19 – empty egg with separated pseudoperculum, ventral view; 20 – anterior pole of egg with two micropylar processes, lateral view; 21 – detail of micropylar process, most exposed view; 22 – detail of part of dorsal egg surface where is egg attached to surface. Scale = 100 μ m for Figs. 17–20; 10 μ m for Figs. 21–22. Letterings: m1, m2 – micropylar processes; p – pseudoperculum.

Chorosoma schillingi. Cap is roughly triangular, egg burster is formed by two elevated, strongly sclerotized ridges, both running laterally from convex central point.

The eggs of *Ch. schillingi* hatch from 8 to 15 days, those of *R. maculatus* from 9 to 15 days after oviposition under common garden conditions in laboratory.

Discussion and conclusion

External morphology of Rhopalidae eggs

Rhopalinae: Rhopalini

Our study of the egg of *Brachycarenus tigrinus* essentially confirms previously published descriptions (PUTSHKOVA 1957; PUTSHKOV 1962, 1986; WHEELER & HOEBEKE 1988; MOULET 1995). Only WHEELER & HOEBEKE (1988) studied the egg chorion using SEM. In keeping with our results, the chorionic surface was covered with raised, circular projections.

The eggs of several other *Rhopalus* species have been studied superficially (see Table 1). Only several more detailed descriptions of the eggs of *Rhopalus parumpunctatus* (Schilling, 1817) have been published (particularly MICHALK 1935; PUTSHKOVA 1955, 1957; PUTSHKOV 1962, 1986). Our results for *R. maculatus* roughly agree with general notes on eggs of *Rhopalus* Stål, 1872. Using SEM study, we detected a completely smooth surface of the chorion. This is the first detailed study of the eggs of a *Rhopalus* species. For comparison, we can use only the descriptions of *R. maculatus* have not developed an attachment stalk originating from the chorion. A similarly shaped structure on some eggs originates from female adhesive secretion (see also below).

The eggs of two genera of Rhopalini, *Brachycarenus* and *Rhopalus*, differ in the following characters. Chorion smooth in *Rhopalus*, whereas that of *Brachycarenus* has a distinct structure formed by rounded tubercles. Micropylar processes are bent posteriorly in *Rhopalus*, but postero-dorsally in *Brachycarenus*; longitudinal ribs, which are conspicuous in *Rhopalus*, are not developed in *Brachycarenus*.

We suggest that our descriptions of eggs of *Brachycarenus* and *Rhopalus* be considered typical for eggs of these genera.

References to descriptions of rhopaline eggs are given in Table 1. On the basis of the literature and our studies, eggs of the Rhopalini can be characterized as follows: oval to beanshaped. Chorion surface of various patterns: completely smooth (*Rhopalus*, probably *Corizus*) to hexagonal (*Liorhyssus*), or with rounded low tubercles (*Brachycarenus*). Pseudoperculum oval in outline, with poorly defined border, its structure identical with surrounding chorion. Two micropylar processes bent roughly posteriad, of various shape, short, dilated basally (*Brachycarenus*), globular (*Rhopalus*), or with slender base and globose apex (*Liorhyssus*). The attachment structure in leglet form was described in *Brachycarenus tigrinus*, *Liorhyssus hyalinus* (Fabricius, 1794) (PUTSHKOVA 1957, ATALAY 1978) and *Rhopalus maculatus*; it was not mentioned in *Corizus hyoscyami* (Linnaeus, 1758) or species of the subgenus *Rhopalus* s. str. (PUTSHKOVA 1957).

Niesthreini

The following description is based on studies of *Arhyssus lateralis*, *Niesthrea louisianica* and *Niesthrea sidae* (Fabricius, 1794) (HAMBLETON 1909, READIO 1928, WHEELER 1977, PASKEWITZ & MCPHERSON 1983). Egg ovoid to oval, widest in middle. Chorion surface with hexagonal reticulation. Pseudoperculum with poorly (*Arhyssus*, *N. sidae*) to well-defined (*N. louisianica*) border. Two micropylar processes short, broad, inconspicuous. Ventral side narrowed opposite center of dorsal side. Short stalk attaching the egg to the substrate develops on dorsal side (as a pedicel in all species). Because detailed infromation on the stalk is unavailable we cannot determine if the stalk is homologous with that in Chorosomatini (see below).

Chorosomatini

Our results confirm and provide a complete description of the *Chorosoma schillingi* egg (for published data, see Table 1). The egg of this species has been used as a 'type egg' of the Rhopalidae (e.g. REUTER 1910; MICHALK 1935, as a 'horizontal type of egg with stalk', SOUTHWOOD 1956; PUTSHKOVA 1955, 1957), and as an egg with a dorsal stalk of attachment to the substrate. The egg of *Ch. schillingi* can be characterized by the chorionic stalk on dorsal side and two S-shaped micropylar processes with a short stem and broadened apex.

The egg of another chorosomatine, *Myrmus miriformis* (Fallén, 1807), has been described in more detail (e.g. BUTLER 1923, MICHALK 1935, PUTSHKOVA 1955). The eggs of *Ch. schillingi* and *M. miriformis* are quite similar. The chorosomatine egg can be characterized as follows. Oval to bean-shaped, with conspicuously convex dorsal side. Chorion surface rough, of complicated pattern, formed from tetragonal, roughly rhomboidal convex elevations, pattern on egg body and on pseudoperculum slightly different. Border-line between egg body and pseudoperculum distinct (*Myrmus*) to much more distinct (*Chorosoma*). Two micropylar processes more conspicuous than in Rhopalini, opening pointed anteriorly, approximately Sshaped, helically bent at apex (*Chorosoma*) or lyre-shaped and toward one another (*Myrmus*). Periphery of egg rounded, without structures on lines between sides. Dorsal side with distinct chorionic attachment stalk approximately in middle. The stalk in *Ch. schillingi* that we describe in detail previously was referred to as a column (MICHALK 1935) or leglet (PUTSHKOVA 1957). The same structure was described in *M. miriformis* and *Agraphopus viridis* (Jakovlev, 1872) as a leglet (PUTSHKOVA 1957).

Harmostini

A brief characterization of the harmostine egg is based on only one published decription, of *Harmostes fraterculus* (Say, 1832) by WHEELER & MILLER (1983). Egg elongate oval, distinct sculpturing on surface of chorion is apparently absent. Two micropylar processes at anterior pole distinct, globular-shaped. Dorsal attachment stalk absent.

We do not have information on eggs of the rhopaline tribe Corizomorphini.

Maccevethini

The following characteristics of eggs of the Maccevethini are based on descriptions of several *Maccevethus* and *Stictopleurus* species (see Table 1). Egg barrel-shaped, dorsal side

convex. Surface of chorion with conspicuous structure, either uniformly reticulated over entire surface (*Stictopleurus*), or chorion with regular hexagonal structure except finer-structured areas on lateral sides and partly on ventral side; irregular hexagonal structure on pseudoperculum (*Maccevethus*). Pseudoperculum roughly circular, distinct. Two micropylar processes either rounded, swollen apically (*Stictopleurus, Maccevethus* partim.), or short, helically bent at apex with opening lateral (*Maccevethus* partim.). Short stalk described and/or illustrated on dorsal side in both genera by PUTSHKOVA (1955, 1957) and MOULET (1995), without detailed information about its origin. For *Maccevethus corsicus*, CANDAN et al. (2004) described direct deposition of eggs to a leaf.

Serinethinae

Characterization of serinethine eggs is based on brief descriptions of *Jadera choprai* Göllner-Scheiding, 1979, *Leptocoris augur* (Fieber, 1781), *Leptocoris mitellata* Bergroth, 1916 and *Leptocoris tagalica* Burmeister, 1834 (see Table 1). Egg, nearly round, with finely and irregularly dimpled chorion, with six (*Jadera*) to 22–45 (*Leptocoris*) micropylar processes arranged in one (*Jadera*) or two (*Leptocoris*) broad circles (11–22 processes in one circle). A short attachment stalk of the egg of *L. augur* was referred to as a pedicel by MALHOTRA (1958) and SCHAEFER & KOTULSKI (2000). The presence of such a stalk has not been mentioned in other serinethine species (e.g. KUMAR 1966).

Characterization of the eggs of family Rhopalidae

The general descriptions of rhopalid eggs, published as characteristic of the family (e.g. SOUTHWOOD 1956, PUTSHKOV 1986) include only the subfamily Rhopalinae. A comparison of descriptions of rhopaline and serinethine eggs indicates that these two groups do not share a common character. The only one character which occurs in Serinethinae (the character has been described for egg of only one species) and Rhopalinae (common only in Chorosomatini) is a stalk on dorsal side attaching the egg to substrate. But we are not certain that these structures are homologous or whether the structure also is mentioned in Coreidae (SOUTHWOOD 1956) (see also below).

Serinethine eggs differ from those of Rhopalinae in having more micropylar processes, minimally six in *Jadera choprai*, as many as 45 in *Leptocoris augur*, in contrast to the standard two in Rhopalinae.

The eggs of Rhopalinae can be characterized as follows. Oval to ovoid or bean-shaped; dorsal side convex, lateral sides slanted toward ventral side, which is only narrow. Surface of chorion mostly with conspicuous structure (smooth chorion observed only in two species of Rhopalini), its pattern formed by rounded tubercles, tetragonal elevations or hexagonal reticulation. Two micropylar processes of variable shape, from short, round, tubercle-shaped to longer structure with swollen or helically bent apex. Both processes apically at anterior pole of egg, one on pseudoperculum, subcentrally or slightly closer to its anterior margin, one on egg body, close to the pseudoperculum margin ('beneath' the pseudoperculum in lateral view). Pseudoperculum mostly indistinctly separated from egg body, or with only slightly to moderately indicated border-line (Chorosomatini, Maccevethini). The dorsal attachment stalk often has been described in rhopalid eggs. However, the chorionic origin of this structure

has been demonstrated only in Chorosomatini; thus it is an inseparable part of the egg shell. The 'hyaline leglet' has been described in several other Rhopalinae (e.g. PUTSHKOVA 1955; PUTSHKOV 1962, 1986). The remaining species do not have a specialized attachment structure (see also below).

Special features of external morphology of rhopalid eggs

Structure of chorion

The egg chorion is secreted by follicle cells, with each unit of the chorion, generally a polygon, originating from an individual follicle cell. SOUTHWOOD (1956) explained modification of chorionic structure as a matter of depth of the follicular pits (shallow \rightarrow hexagonals, deeper \rightarrow punctation). Chorionic structure is commonly highly complicated in the Pentatomoidea (e.g. DAVIDOVÁ-VILÍMOVÁ 1987, DANIELCZOK & KOCOREK 2003, MATESCO et al. 2009), as well as in other taxa, e.g. Nabidae (CHIAPPINI & REGUZZI 1998), Reduviidae (WOLF & REID 2000, SCHAEFER & WOLF 2003). Because the pattern of the chorionic surface is species-specific (e.g. SOUTHWOOD 1956), it can be used as a good diagnostic character (e.g. BUNDY & MCPHERSON 2000).

The chorionic structure has been studied by SEM in only two rhopalid species, *Brachy-carenus tigrinus* (WHEELER & HOEBEKE 1988; this paper) and *Maccevethus corsicus* (CANDAN et al. 2004). It has been described as hexagonal with a slight cavity in the middle of each hexagon.

We describe the chorionic surface of *Ch. schillingi* as bearing tetragonal, approximately rhomboidal convex elevations. This pattern roughly agrees with the line drawings of BUTLER (1923) and MICHALK (1935). PUTSHKOVA (1957) and PUTSHKOV (1986) described the chorionic structure in *Ch. schillingi* as ranging from smooth to conspicuously structured. Such intraspecific variability, however, seems unlikely and to require verification. The variable structure reported might have been due to the use of only basic optical equipment.

While patterns of the chorionic surface of *B. tigrinus* and *Ch. schillingi* fit known variation within the Heteroptera, we discovered a unique structure in *R. maculatus*: the chorion entirely glossy, smooth, without any microstructure. As for as we know, such a condition has not previously been recognized in species of Pentatomomorpha. The chorion can be almost smooth in some Heteroptera species, but a distinct structure actually occurs on an otherwise smooth chorion, e.g. polygons formed from spines in some Pentatomidae: Asopinae (WOLF & REID 2004), or sporadic low-rounded tubercles of different size in the scutellerid *Psacasta exanthematica* (Scopoli, 1763) (CANDAN & SULUDERE 2003). BUNDY & MCPHERSON (2000) described the chorion of some Pentatomidae as 'smooth', but it is not under high magnification. The chorion is smooth only in comparison with that of other species.

Why might the chorion of *R. maculatus* be completely smooth? In comparison with *Ch. schillingi*, which has a structured chorion, *R. maculatus* deposits eggs on hygrophilous host plants, e.g. on *Comarum palustre* in peat-bog habitats, whereas *Ch. schillingi* lays eggs on grasses in dry meadows or steppes. COBBEN (1968) mentioned that heteropteran eggs can resist flooding when in diapause. However, we suggest that the eggs with a distinct structure rather than a smooth chorion (to keep air on its surface) is an adaptation to a wet habitat.

Another explanation of differences in chorionic structure in these two species is their different overwintering habits. While *R. maculatus* overwinters as adults, *Ch. schillingi* overwinters as eggs, as do other chorosomatines, e.g. *Myrmus* species.

Shape and size of eggs

Heteropteran eggs have three proportions: length, width and height. PUTSHKOVA (1957) defined and suggested a so-called coefficient of flattening to characterize eggs, i.e. proportion of height to length. The coefficient is smaller in elongated eggs, higher in short, robust eggs. This coefficient provides information on egg shape and can express similarity in shape better than individual proportions.

The coefficient of flattening of rhopalid eggs falls within known variation in coreoid eggs. The coefficients are as follows: *B. tigrinus* 0.3–0.4, *Maccevethus corsicus* Signoret, 1862 0.6 and *Rhopalus parumpunctatus* 0.7 (PUTSHKOVA 1957). The coefficients we determined for *Ch. schillingi* 0.52 (0.45–0.55) and *R. maculatus* 0.52 (0.48–0.56) are identical and agree with those of other Rhopalidae.

The egg size of the three species we studied falls within the variation known for other rhopalids. The largest known egg is that of *Stictopleurus punctatonervosus* (Goeze, 1778), 1.5 mm (MOULET 1995), rather than species with the largest adults, i.e. *Chorosoma schillingi* (egg only 1.23 mm, our results; MOULET 1995). *Maccevethus errans errans* (Fabricius, 1794) (MOULET 1995) and *Rhopalus distinctus* (Signoret, 1859) (PUTSHKOVA 1957) have the smallest eggs (0.8 mm). The size of eggs is not positively correlated with the body size of a female. The phenomenon is seen in *Ch. schillingi*, whose adults are as much as two times longer than other Rhopalinae that have been studied, but their eggs are of identical size. A preference for grasses as host plants represents an autapomorphy of Chorosomatini; their narrow, elongate body is an adaptation to living on Poaceae. Chorosomatine eggs, which are only moderately large within Rhopalinae, might represent an adaptation to living on narrow grass leaves: larger eggs might more readily fall from host plants.

Attachment system of eggs

SOUTHWOOD (1956) mentioned the occurrence of an attachment stalk as a specific feature of rhopalid eggs. He studied in detail (in sections) the stalk in *Chorosoma schillingi* and concluded that the '... stalk consists of chorion, almost entirely exochorion' (see also COBBEN 1968).

Consequently, PUTSHKOVA (1957) characterized eggs of Rhopalidae as having a hyaline leglet that originates from a hyaline secretion of the female. Its variation in shape was explained by the use of different amounts of secretion, which stiffens into different final shapes. PU-TSHKOVA (1957) did not differentiate the structure of *Ch. schillingi*, but she mentioned a leglet in several other genera: *Liorhyssus, Brachycarenus* (Rhopalini), *Maccevethus, Stictopleurus* (Maccevethini), *Chorosoma, Myrmus*, and *Agraphopus* (as *Leptocerea*) (Chorosomatini).

A short stalk also has been observed in other Rhopalini taxa, such as *Corizus hyoscyami* (ZWALUWENBURG 1944) and *Rhopalus subrufus* (Gmelin, 1788) (MOULET 1995). CANDAN et al. (2004) was incorrect in noting that the dorsal surface of the egg of *Maccevethus corsicus* is attached to a leaf 'by the help of salivary secreted by female' (*sic*!).

Our results clarify the origin of the attachment stalk in rhopalid eggs. Only in *Ch. schillingi* is the stalk a part of the chorionic surface of the egg. A female adhesive secretion deposited on the apex fixes the egg to the substrate. BUTLER (1923) correctly described the stalk of *Ch. schillingi* as '... composed entirely of the outermost and structureless layer of chorion'. MICHALK (1935) mentioned this structure in *Ch. schillingi*, as well as in *Myrmus miriformis*. MOULET (1995) demonstrated the presence of a stalk in *Ch. schillingi*.

We observed that eggs of *Rhopalus maculatus* are mostly deposited directly on the substrate by the dorsal side with the aid of a thin film of adhesive secretion. The egg's dorsal side lacks a distinct chorionic structure similar to the attachment stalk described above. We found only remnants of the secretion in the area of the egg attached to the surface. Some of the eggs (about 12 %), showed a more extensive columnar structure roughly similar to the stalk in *Ch. schillingi*. This structure can be removed from the egg surface almost without leaving a trace. We demonstated that it is not a part of the egg chorion. The shape of this columnar structure varies, in contrast to a well-developed attachment stalk. We suggest that this variation is due to a female's producing a variable amount of secretion. With a small amount, the egg is glued by a thin film, but with a larger amount, the secretion stiffens to form a short column. The different behaviour by a female, and thus variation in the amount of secretion produced, might be the result of either internal or external stimulation.

Reports of a stalk/pedicle in rhopalid eggs probably do involve true chorionic structures, but instead pertain to structures resulting from the stiffening of adhesive secretion. A chorionic attachment stalk occurs in Chorosomatini, but we do not have enough data to resolve the origin of the stalk in eggs of Niesthreini, Maccevethini and Serinethinae.

Oviposition and egg hatch

All rhopalid eggs are deposited parallel to the surface and touch the surface directly or make contact with the substrate indirectly by way of an attachment stalk.

MICHALK (1935) defined ten types of egg deposition in Heteroptera. Rhopalid eggs were classified either as 'horizontally glued' (e.g. the reduviid *Coranus subapterus* (DeGeer, 1773)), or 'horizontally glued with column' (e.g. *Ch. schillingi*). PUTSHKOVA (1955, 1957) classified rhopalid eggs as the rhopaloid type. COBBEN (1968) recognized only three types of egg deposition in Heteroptera, with those of rhopalids belonging to a 'superficial, horizontal position' type. This type is considered the most general and thus original = ancestral. All known rhopalid eggs fit this type of oviposition.

Eggs deposited singly are thought to represent the ancestral condition, whereas eggs laid in groups (batches) are considered to be a more advanced condition (COBBEN 1968).

Our observations on oviposition behaviour of *Ch. schillingi* and *B. tigrinus* agree with published data (see Table 1). In the case of reared females of *Ch. schillingi*, the small number of eggs in a batch might be either natural or caused by laboratory conditions. We found that *R. maculatus* deposits eggs singly.

We characterize the oviposition behaviour of rhopalid tribes as follows:

<u>Rhopalini</u>. *Liorhyssus hyalinus* (KIRKALDY 1907, READIO 1928, SCHWOERBEL 1956, PUTSHKOVA 1957): Eggs deposited in mass, not touching each other, identically oriented, parallel one to

another, the number per batch varying from five to 56, but typically 20 to 30. Single eggs are rare. *Corizus hyoscyami* (ZWALUWENBERG 1944; PUTSHKOVA 1955, 1957; SCHWOERBEL 1956): Similar to *L. hyalinus*, the number of eggs per batch ranged from five to 18. *Brachycarenus tigrinus* (PUTSHKOVA 1955, 1957; SOUTHWOOD 1956; COBBEN 1968; WHEELER & HOEBEKE 1988; present paper): Eggs deposited singly. *Rhopalus* species (MICHALK 1935, PUTSHKOVA 1957, SOUTHWOOD & LESTON 1959, present paper): Eggs deposited singly; in *R. parumpunctatus* eggs laid in ones or twos.

Brachycarenus and Rhopalus have an ancestral type of oviposition. Oviposition in R. parumpunctatus can be classified as a precursor to a more advanced type having eggs in mass, as seen in Corizus and Liorhyssus. Corizus and Liorhyssus groups of eggs are of simple character, irregular shape, with eggs not touching each other.

Niesthreini. Arhyssus lateralis (HAMBLETON 1909, READIO 1928, PASKEWITZ & MCPHERSON 1983): Eggs laid singly or in small clusters of two to 14. Niesthrea species (READIO 1928, WHEE-LER 1977): Eggs in nearly circular or irregular-shaped clusters of seven to 20 (aver 14).

Niesthreini deposit eggs in relatively small, not rigid clusters.

<u>Chorosomatini</u>. *Chorosoma schillingi* (MICHALK 1935, PUTSHKOVA 1957, SOUTHWOOD & LES-TON 1959, present paper): Eggs deposited in a regular batch, in one row or two spike-shaped rows, the batch sometimes irregular, with six to 20 eggs. SOUTHWOOD & LESTON (1959) also described egg deposition as single. *Myrmus miriformis* (MICHALK 1935; PUTSHKOVA 1955, 1957; SOUTHWOOD & LESTON 1959; PUTSHKOV 1962): Eggs are laid mostly in ones or twos, or in a batch in one row of two to three to 19.

Both chorosomatine genera show greater variability in oviposition behaviour. The eggs are in most cases laid singly or in twos, sometimes in one row, often in a spike-shaped batch.

Harmostini. Harmostes fraterculus (WHEELER & MILLER 1983): Eggs usually are deposited singly.

<u>Maccevethini</u>. *Maccevethus* species (PUTSHKOVA 1957, CANDAN et al. 2004): Eggs are laid in a usually spike-shaped batch of eight to 40. *Stictopleurus punctatonervosus* (PUTSHKOVA 1955, 1957; MOULET 1995): Eggs are deposited either singly or in irregular groups of two to five.

Oviposition differs in the two maccevethine genera studied. *Stictopleurus* lays single eggs or a tiny group of eggs, whereas *Maccevethus* deposits a spike-shaped egg batch.

Serinethinae. Boisea trivittata (Say, 1825) (SCHAEFER & KOTULSKI 2000): Eggs are laid in masses of about 11. Leptocoris species (MALHOTRA 1958, KUMAR 1966, SCHAEFER & KOTULSKI 2000): Eggs are deposited singly or in batches of as many as 16.

Serinethinae deposit eggs singly or in masses of maximally 16.

We do not have complete data on the oviposition behaviour of all rhopalid taxa. It is possible that all oviposition types are found in all higher taxa, from a primitive condition of eggs laid singly to grouped in batches. In Rhopalini, two types are found: eggs deposited singly or in unorganized batches. Only a more advanced type is seen in Niesthreini: eggs laid in clusters. In the following three, presumably advanced rhopalid taxa - Chorosomatini, Maccevethini and Serinethinae - we find the primitive condition, single eggs, in addition to the most advanced one, eggs deposited in batches of regular shape, mostly in a spike.

Egg burster. The rhopalid egg burster was described in detail by PUTSHKOVA (1957). Our observations of this structure in *Ch. schillingi* and *R. maculatus* are typical of the condition in other Rhopalidae.

Use of rhopalid eggs in diagnostic keys

Egg characters have been used in diagnostic keys to genera and/or species of Rhopalidae. The most detailed keys are those of PUTSHKOVA (1957) and PUTSHKOV (1962, 1986), which were published in Russian or Ukrainian and modified by MOULET (1995). The following characters were used in the keys: structure of chorionic surface, size and shape of micropyles, size and shape of the entire egg, and absence or presence of a dorsally attached stalk. However, for an accurate description of rhopalid eggs, it is necessary to study them by SEM or use other types of high-optical instruments.

External egg morphology in relation to rhopalid phylogeny

Hypotheses of rhopalid phylogeny, a taxon originally considered a subfamily of the Coreidae, were summarized by DAVIDOVÁ-VILÍMOVÁ et al. (2000). The subfamily Serinethinae generally is considered the most advanced rhopalid taxon and the subfamily Rhopalinae the most plesiomorphic. It is generally accepted that the tribes Rhopalini and Niesthreini are closely related and the most generalized within Rhopalinae. Successively more advanced are Chorosomatini – Harmostini – Corizomorphini, with Maccevethini most advanced and closely related to the subfamily Serinethinae.

Only three egg characters that have been analyzed can be used to infer rhopalid phylogeny. The occurrence of the chorionic attachment stalk is clearly an advanced condition, its absence representing the plesiomorphic condition (SOUTHWOOD 1956, COBBEN 1968). Micropylar processes: Only one micropylar process exists originally in Heteroptera, located at the cephalic pole. In Pentatomomorpha, a small number of micropylar processes is a plesiomorphic condition and a higher to high number of processes more advanced (COBBEN 1968). SOUTHWOOD (1956), however, considered two micropylar processes as a specialized character of rhopalid eggs in comparison to Coreoidea. We accept COBBEN's (1968) approach to polarization of these character states. Arrangement of deposited eggs: Attachment horizontal to the substrate is the ancestral practice in heteropteran oviposition and thus is a primitive trait (COBBEN 1968).

All Rhopalidae share the primitive type of egg attachment during oviposition.

The egg characters of Serinethinae confirm its position as the most advanced taxon within the family. They have more than two micropylar processes, minimally six, maximally as many as 45, arranged in one or two broad circles, which represents an apomorphic condition. The short stalk mentioned in descriptions of the eggs has not been described in any detail. We cannot determine if the described structure is of chorionic origin, as in the Chorosomatini, and thus represents an apomorphic state.

All eggs of the Rhopalinae show the primitive condition, only two micropylar processes developed, one at the cephalic = anterior pole. The eggs of the advanced tribe Maccevethini share some specific characters. The stalk is mentioned in egg descriptions, but again without details. Maccevethine eggs have a distinct pseudoperculum, chorion of hexagonal structure

and micropylar processes of complicated shape. All these states also are found in other taxa of the Rhopalinae and are not specific for this tribe. The only character characteristic for Maccevethini is the egg barrel-shaped, more robust than in other Rhopalinae. The eggs of Chorosomatini share an advanced condition, the attachment stalk of chorionic origin, which represents a more specialized manner of egg attachment. Their eggs also have micropylar processes that are the most complicated within the Rhopalinae, namely a chorion of tetragonal structure with a distinct border-line on the pseudoperculum. Only scant data are available on eggs of the tribe Harmostini; the attachment stalk is not developed. Most eggs characters of the Rhopalini are primitive, e.g. pseudoperculum poorly defined. The structure attaching egg to substrate can be in a shape similar to the chorionic stalk, but it originates from female adhesive secretion. Only in this tribe did we find a completely smooth chorionic surface. We cannot, however, decide whether this is a primitive or an advanced character state. The scant data available on eggs of the tribe Niesthreini are identical with those for the Rhopalini, and except for the smooth chorion, they do not show any distinct character. Also the egg characters support a close relationship between these two tribes. Egg characters generally support the accepted phylogeny (SCHAEFER & CHOPRA 1982) for subfamilies and tribes of the family Rhopalidae.

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