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Taxonomy of the genera *Scaeva*, *Simosyrphus* and *Ischiodon* (Diptera: Syrphidae): Descriptions of immature stages and status of taxa

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Abstract. A review of all known descriptions of immature stages of the species of the genera *Scaeva* Fabricius, 1805, *Ischiodon* Sack, 1913 and *Simosyrphus* Bigot, 1882 is presented using SEM illustrations. The third instar larval and/or pupal morphology of *Scaeva dignota* (Rondani, 1857), *Scaeva mecogramma* (Bigot, 1860) and *Simosyrphus grandicornis* (Macquart, 1842) are newly described. All species of the genera studied in this paper are very similar for all the studied characters of their immature stages, including the chaetotaxy. Molecular characters of the mitochondrial *cox1* gene (1128bp) were used for inferring relationships of the studied taxa. The nuclear internal transcribed spacer 2 (ITS2) was additionally applied for species delimitation of the closely related species *Scaeva selenitica* and *S. dignota*. The Palaearctic *Scaeva* species could be split into two groups based on the analysis of morphology of posterior respiratory process. These groups were previously diagnosed as *S. selenitica*-group [i.e., *S. selenitica* (Meigen, 1822), *S. dignota* (Rondani, 1857), *S. mecogramma* (Bigot, 1860)] and *S. pyrastri*-group [i.e., *S. pyrastri* (Linnaeus, 1758), *S. albomaculata* (Macquart, 1842), *S. latimaculata* (Brunetti, 1923)]. *Semiscaeva* Kuznetzov, 1985 and *Scaeva* Fabricius, 1805 are the available names for these two natural groups that should be classified as subgenera; the former name is proposed for *S. selenitica*-group and the latter for *S. pyrastri*-group. *Mecoscaeva* Kuznetzov, 1985 syn. n. is transferred as a junior synonym of the subgenus *Semiscaeva* Kuznetzov, 1985 according to the principle of the first reviser. Based on the analysis of immature stages, the generic name *Ischiodon* Sack, 1913 syn. n. is proposed as a junior synonym of the genus *Simosyrphus* Bigot, 1882. The similarity of immature stages between *Scaeva* s. str. and *Simosyrphus grandicornis* Macquart, 1842, *Simosyrphus aegyptius* (Wiedemann, 1830) comb. n. and *Simosyrphus scutellaris* (Fabricius, 1805) comb. n. is discussed. All the proposed subgeneric and generic taxa based on morphological studies received high support employing molecular characters.

INTRODUCTION

One of the major larval feeding modes of syrphids is predation. The 1800+ species of Syrphinae make up a large proportion of the species richness of hoverflies, about 35% of the family. Virtually all of them feed as larvae on soft-bodied Hemiptera (sensu Sörensen et al., 1995) although some species also attack other arthropods (see Rojo et al., 2003). The species of genera *Scaeva* Fabricius, 1805, *Ischiodon* Sack, 1913 and *Simosyrphus* Bigot, 1882 are predatory syrphids with an important role in the bio-control of aphid pest in different areas of the world (e.g. Lal & Haque, 1965; Schmutterer, 1972; Mukhitdinov, 1985; Singh & Mishra, 1988; Sharma & Bhalla, 1991; Xiong & Dong, 1991; Ekukole & Ajayi, 1995; Soleyman-Nezhadiyan & Laughlin, 1998). Descriptions of immature stages of Syrphini are useful for ecological studies, e.g. as a method for comparing the role of various natural enemies of aphids (Láska, 1984) or the study of species relationships, where they provide additional useful characters for phylogenetic studies, which presently are based mainly on characters of adults.

In 1985 two revisions of the genus *Scaeva* were published independently by Dušek & Láska (1985) and Kuznetzov (1985). However, these two revisions are quite different in species conceptions and in subgeneric classification. Recent authors usually follow the concept of Dušek & Láska (e.g. Speight, 2003), but up to now no nomenclatorical acts have been published to clarify this situation. The defence of Dušek & Láska's concept (1985) is also part of our contribution with the use of newly available data obtained for this study.

According to Kassebeer (1999) and Thompson (2003), 19 valid names of the genus *Scaeva* exist at present. These species of *Scaeva* are mainly distributed in the Palaearctic (with two species reaching the Oriental region and one species the Nearctic region) and Neotropical (four species) regions. The genus *Ischiodon* comprises three species only (one endemic of the Cape Verde Islands, one mainly present in Africa and one in the Oriental-Austral region), and of the genus *Simosyrphus* (exclusive to the Australian region, including Pacific) only one species is known. These three genera – *Scaeva*, *Ischiodon*, *Simosyrphus* Dušek & Láska (1985) ranged into *Scaeva* group.

The single species of *Simosyrphus* bears a strong resemblance to the species of *Ischiodon*, with which it has often been confused (e.g. Bryan, 1934). In his famous world revision of the genera of the Syrphini, Vockeroth (1969) was at first inclined to refer all the species of the genera *Ischiodon* and *Simosyrphus* to a single genus despite the apparent differences in the male terminalia. He finally concluded that both genera are related but not congeneric. This author also discussed the close relationship between *Scaeva* and *Eupeodes* Osten Sacken, 1877 (including *Metasyrphus* Matsumura, 1917) but did not support a relation between *Scaeva* and *Simosyrphus*. Dušek & Láska (1985) first diagnosed these taxa including *Ischiodon* and *Simosyrphus* as a natural group, using both larval and adult morphology. Monophyly of the genera *Scaeva*, *Eupeodes* and *Ischiodon* was recovered in the parsimony analysis of Palaearctic Syrphidae larvae (Rotheray & Gilbert, 1999), but the larvae of the genus *Simosyrphus* and some *Scaeva* species of the Mediterranean and Oriental regions were undescribed and thus not included. In the present work we redescribe or describe the third instar larvae and/or puparia of the species of *Scaeva*, *Ischiodon* and *Simosyrphus* and give a key to known immature stages of the species.

Additionally, in the present study we use DNA sequences of two genes, the mitochondrial cytochrome c oxidase subunit I (hereafter *cox1*), and the nuclear ribosomal internal transcribed spacer two (ITS2) for understanding the species limits of very closely related taxa. The mitochondrial *cox1* has been used and proven to be valuable for inferring species-level phylogenies of other syrphid genera (Ståhls & Nyblom, 2000; Pérez-Bañón et al., 2003), as well as for other insects (e.g. Caterino & Sperling, 1999). Recent findings, however, indicate that the *cox1* might be too slowly evolving to be informative between very closely related species (recent speciation), as interspecific divergences are close to zero (Milankov et al., 2005; Rojo et al., 2006; G. Ståhls, unpubl. data). Hebert et al. (2003), and Megens et al. (2004) showed that pairwise uncorrected divergence values for *cox1* were generally greater than 3% between species of Lepidoptera in general. Both studies also report genetically distinct but very low divergences of the *cox1* (0.6–2.4%) for congeneric species pairs, suggesting these low values as indicative of very recent origins of species. The nuclear non-coding ITS2 is a rapidly evolving region and has proved useful for comparing closely related insect species, subspecies or populations in insects (e.g. Álvarez & Hoy, 2002), indicating that the mutation rate could ordinarily be higher for the ITS2 than for any mitochondrial (protein coding) gene. We explored the utility of both gene regions for the specific study of the closely related species pair *Scaeva dignota* (Rondani, 1857) and *S. selenitica* (Meigen, 1822), and to use the *cox1* for inferring the phylogenetic relationships among the taxa of this study using seven representatives.

Proposed taxonomical changes are mainly based on the study of immature morphology, but we also find the molecular characters highly informative to address these questions. Genotypes can be expected to express variation for recently diverged species even when morphological characters still show no variation or it is difficult to observe. The adult morphologies are discussed in relation to results obtained using the two above mentioned character sets. The final conclusions as well as proposed taxonomical changes, however, are established in light of all character sets and long term study of Syrphini. The discussion deals also with some paradoxes in relation to evolution of larval and adult characters.

MATERIAL AND METHODS

Morphological studies

We have used numerous larvae and puparia of the *Scaeva* species and several puparia of the *Simosyrphus* and *Ischiodon* species stored in the entomological collection of the Universidad de Alicante, Alicante, Spain (CEUA) and Department of Zoology and Anthropology, Olomouc, Czech Republic (UP).

Third instar larvae and empty puparia were studied. Larvae were either reared in laboratory from eggs or were obtained by searching in the field. Collected gravid females (see UP material) were put in separated boxes with a plantlet of *Vicia faba* (Fabaceae) previously infested with the pea aphid *Acyrthosiphon pisum* (Harris, 1776) (Hemiptera: Aphidoidea). The methodology for laboratory breeding of the aphids was adopted from Department of Entomology at the Academy of Sciences of the Czech Republic (České Budějovice). Syrphid field-collected larvae were usually fed with aphids from the same colony where they were collected. Rearing took place in a growth chamber at 16–22°C, 80 ± 5% RH with a constant photo regime of 15L : 9D (CEUA material) or at 22–25°C with 16L : 8D (UP material). Puparia were isolated in individual Petri dishes and inspected daily until the adults emerged.

Third instar larvae were selected for preservation after the hindgut was emptied. Obtained larvae were fixed by immersion in boiling water and boiling gently for about four minutes to extend them; they were preserved in 70% alcohol afterwards and part of the obtained larvae were lyophilised. To study the prothorax, mesothorax and metathorax morphology, we extended these parts by lightly pressing the first abdominal segments.

Descriptions are based on preserved larvae and/or puparia. Larval characters were checked against living specimens, when possible. Dimensions were measured on preserved material using a binocular microscope (Leica Wild M8) with an eyepiece micrometer and illustration made with a drawing tube. The width of the posterior respiratory process (below PRP) was measured from anterolateral points of carinae I in posterodorsal view (see Fig. 6).

Terminology used for descriptions of larvae and pupae follows Dušek & Láska (1964). The term orificium (Vimmer, 1925) was used instead of spiracular slits, and the term periorificial ornamentation was used instead of interspiracular ornamentation that is used in papers by other authors, following Bhatia's (1939) fundamental work on morphology and anatomy of aphidophagous syrphid larvae. The positions of the sensillae were numbered from the dorsal to the ventral surface of each segment (see Fig. 4), as decribed by Rotheray (1991).

Molecular studies

DNA was extracted usually from legs (of a single individual) of frozen specimens or from specimens preserved in 70–95% alcohol (Table 1). Adults were conserved as DNA voucher specimens. DNA was extracted using the Nucleospin Tissue Kit

TABLE 1. List of specimens used for DNA analysis. X denotes obtained sequence not submitted for GenBank.

	Genus *Scaeva*, subgenus *Semiscaeva*			*Cox1*	ITS2
S100	*Scaeva dignota* (Rondani)	Greece, Lesbos island, iv.2001, leg. S. Rojo & C. Pérez	CIBIO	X	X
S107	*Scaeva dignota* (Rondani)	Greece, Lesbos island, iv.2001, leg. S. Rojo & C. Pérez	CIBIO	AY603766	X
S135	*Scaeva dignota* (Rondani)	Italy, South Tirol, Val Venosta, vii.2001, leg. G. Ståhls	ZMH	X	DQ158893
S195	*Scaeva dignota* (Rondani)	Greece, Lesbos island, iv.2001, leg. S. Rojo & C. Pérez	CIBIO	X	X
S196	*Scaeva dignota* (Rondani)	Greece, Lesbos island, iv.2001, leg. S. Rojo & C. Pérez	CIBIO		DQ158894
S198	*Scaeva dignota* (Rondani)	Spain, Alicante, 17.vi.2001, leg. S. Rojo & C. Pérez	CIBIO	X	X
S199	*Scaeva dignota* (Rondani)	Spain, Alicante, 26.vi.2001, leg. S. Rojo & C. Pérez	CIBIO	X	
S66	*Scaeva selenitica* (Meigen)	Czech Republic, distr. Chomutov, Lestkov, 21.iv.2000, leg. L. Mazánek	CIBIO	X	X
S69	*Scaeva selenitica* (Meigen)	Czech Republic, distr. Ostrava, Polanecký les, 3.iv.2000, leg. T. Kuras	CIBIO	AY603764	X
S126	*Scaeva selenitica* (Meigen)	Italy, South Tirol, Val Venosta, vii.2001, leg. G. Ståhls	ZMH	X	X
S127	*Scaeva selenitica* (Meigen)	Italy, South Tirol, Val Venosta, vii.2001, leg. G. Ståhls	ZMH	X	DQ158895
S134	*Scaeva selenitica* (Meigen)	Italy, South Tirol, Val Venosta, vii.2001, leg. G. Ståhls	ZMH	X	DQ158896
	Subgenus *Scaeva* s. str.				
S105	*Scaeva albomaculata* (Macquart)	Greece, Lesbos island, iv.2001, leg. S. Rojo & C. Pérez	CIBIO	AY603765	
S97	*Scaeva pyrastri* (Linnaeus)	Greece, Lesbos island, iv.2001, leg. S. Rojo & C. Pérez	CIBIO	AY603767	
	Genus *Simosyrphus*				
S288	*Simosyrphus grandicornis* Macquart	Australia, Brisbane, 5.x. 2002, leg. H. Hippa	ZMH	AY603770	
S157	*Simosyrphus* (=*Ischiodon*) *scutellaris* Fabricius	Hong-Kong, 7.x.2001, leg. D. Iliff	ZMH	AY603768	
S361	*Simosyrphus* (=*Ischiodon*) *aegyptius* Wiedemann	Morocco, Guelmim, 28.xii.2002, leg. J.-H. Stuke	ZMH	AY603769	
Outgroup	*Eupeodes (Lapposyrphus) lapponicus* (Zetterstedt)	Czech Republic, 13.v.2000, leg. L. Mazánek	ZMH	DQ158897	

(Machery-Nagel, Düren, Germany) according to manufacturer's protocols, and resuspended in 50 µl of ultra-pure water.

PCR's were carried out in 25 µl reactions containing 1–2 µl DNA extract, 1 µl of each primer (at 10 pmol/ml), 0.25 µl of Amplitaq DNA polymerase (5U/µl), 2 µl 2.5 mM $MgCl_2$, 2.5 µl 10X Buffer II (Applied Biosystems, Foster City, CA, USA) and 4 µl 200 mM dNTP (GeneAmp, Applied Biosystems) and water. Thermocycler conditions were initial denaturing at 95°C 2 min, 29 cycles of 30 s denaturing at 94°C, 30 s annealing at 49°C, 2 min extension at 72°C, followed by a final extension of 8 min at 72°C. PCR products were purified using the GFX PCR Purification Kit (Amersham Biotech, Little Chalfont, UK) and then sequenced (using the same PCR primers) in both directions using the Big Dye Terminator Cycle Sequencing Kit (Applied Biosystems) at one-fourth of the recommended volumes on ABI PRISM 377 and ABI 310 automated DNA sequencers. The primers used for amplifying and sequencing the *cox1* and ITS2 fragments are listed in Table 2. Sequences were edited and assembled using Sequence Navigator™ (version 1.01, Applied Biosystems). We produced nucleotide sequences of the *cox1* and ITS2 genes of several specimens of the closely related species *Scaeva dignota* and *S. selenitica*, in addition to other species of the genus *Scaeva* (see Table 1).

We used the obtained sequence data to calculate uncorrected pairwise *cox1* sequence divergences for *S. dignota* and *S. selenitica*. We determined the ITS2 sequences of six specimens of *S. dignota* and five specimens of *S. selenitica* (Table 1), and these were manually aligned to identify sequence variation for these taxa.

We performed a parsimony analysis using one *cox1* sequence to represent each taxon included in this study and using equal weights with the computer program Nona version 2.0 (Goloboff, 1993) to study the relationships of species-groups in *Scaeva*, and the relationships among *Scaeva, Ischiodon* and *Simosyrphus*. Bremer support values (Bremer, 1994) were calculated using Nona by successively increasing the number of trees retained (hold 1000; suboptimal 1; find*: followed by hold 2000; suboptimal 3; find*: etc.), to avoid overestimating the values. Bootstrap values were calculated using Winclada (Nixon, 2002) with 1000 pseudoreplicates. *Eupeodes* (*Lapposyrphus*) *lapponicus* (Zetterstedt, 1838) was used as outgroup.

TAXONOMIC ACTIONS

On the basis of new data provided by this study and long term study of Syrphini we propose in this paper the following arrangement of taxa.

Scaeva Fabricius, 1805

Palaearctic *Scaeva* species can be clearly split into two groups based mainly on the morphology of PRP. The first group corresponds to the S. *selenitica*-group of Dušek & Láska (1985), and second group to the S. *pyrastri*-group

TABLE 2. Primers used for amplifying and sequencing the *cox1* and ITS2 fragments.

Primer	Sequence	Source
TL2-N-3014	5'-TCCAATGCACTAATCTGCCATATTA-3'	Simon et al., 1994
C1-S-1718	5'-GGAGGATTTGGAATTGATTAGTTCC-3'	Simon et al., 1994
C1-J-2183	5'-CAACATTTATTTTGATTTTTTGG-3'	Simon et al., 1994
ITS2A (f)	5'-TGTGAACTGCAGGACACAT-3'	Beebe & Saul, 1995
ITS2B (r)	5'-TATGCTTAAATTCAGGGGGT-3'	Beebe & Saul, 1995

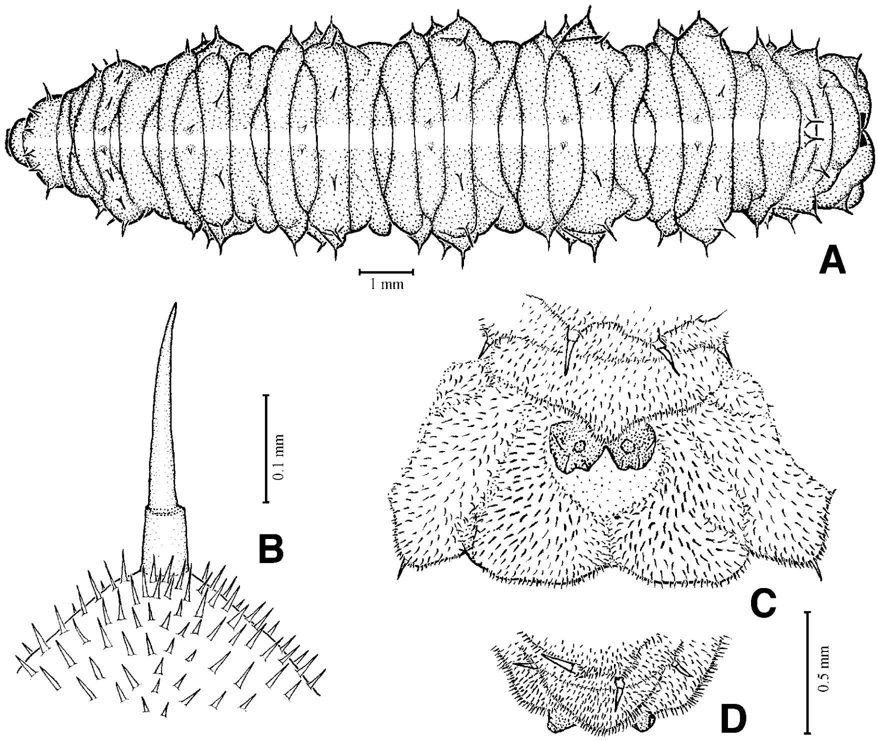

Fig. 1. A, B: Third instar larva of *Scaeva selenitica*. A – dorsal habitus; B – segmental spine 2^{A6} with its fleshy projection. C, D: *Scaeva albomaculata*. C – posterior end of the third instar larva; D – posterior end of puparium.

of Dušek & Láska (1985). These alleged natural groups were diagnosed by Dušek & Láska (1985: p. 226) using both adult and larval characters. We propose to classify them as subgenera. For genesis of proposed subgeneric names see discussion.

Subgenus *Semiscaeva* Kuznetzov, 1985

[= *S. selenitica* group sensu Dušek & Láska (1985: 226)]

Semiscaeva Kuznetzov, 1985: 412 (as subgenus of *Scaeva* Fabricius, 1805). Type species *Catabomba odessana* Paramonov, 1924 (orig. des.) = S. *dignota* (Rondani, 1857).

Mecoscaeva Kuznetzov, 1985: 418 (as subgenus of *Scaeva* Fabricius, 1805). Type species *Lasiophthicus mecogramma* Bigot, 1860 (monotypy). Syn. n. (first reviser).

Subgenus *Scaeva* s. str.

[= *S. pyrastri* group sensu Dušek & Láska (1985)]

Scaeva Fabricius, 1805: 248. Type species: *Musca pyrastri* Linnaeus, 1758 (des. Curtis, 1834: pl. 509).

Synonymy of *Simosyrphus* Bigot, 1882 and *Ischiodon* Sack, 1913

Vockeroth (1969) provided differential diagnosis and detailed descriptions of adult characters of both genera. The new data of this paper, larval and pupal morphology and molecular data confirm the very close relationship of *Simosyrphus* and *Ischiodon*. We propose their synonymy and a sister-group relationship with the genus *Scaeva*.

Simosyrphus Bigot, 1882

Simosyrphus Bigot, 1882: 68. Type species *Syrphus grandicornis* Macquart, 1842 (sub. des. Hull, 1949: 291).

Ischiodon Sack, 1913: 6. Type species: *Ischiodon trochanterica* Sack, 1913 (monotypy) = *I. scutellaris* (Fabricius, 1805). Syn. n.

DESCRIPTION OF IMMATURE STAGES

Scaeva Fabricius, 1805

Third instar larva

Length 12–18 mm, maximum width 3.0–4.0 mm. **Overall appearance:** Oval in cross-section with a little flattened ventral surface, tapering anteriorly and slightly truncate posteriorly. Dorsal habitus wrinkled (Fig. 1A), slightly serrate owing to fleshy projections with segmental spines (sensillae with setae). Colour pattern variable in ground colour even at intraspecific level (green, brown or pink) with a median dorsal white, cream or pink stripe. Prothorax and mesothorax normally retracted into metathorax. Boundaries between segments obscured by secondary grooves and folds in integument (Fig. 1A). Abdominal segments usually bearing five secondary folds. The pattern of segmental spines is very useful for orientation in primary segmentation, mainly the position of the segmental spines of each side of abdominal segments. Pairs 1 and 2 of segmental spines both located on second fold in metathorax and first abdominal segment; in other abdominal segments, pair 2 of segmental spines located just on the next fold (Fig. 1A). Segmental spines not pigmented, fully developed (0.15–0.28 mm long), with wide base (about 1/3 length of spine) and a narrow apical part (Fig. 1B). Integumental vestiture distinct in most species, of cuticle colour or brown pigmented, smaller in groves and on ventral surface. Dorsal body sur-

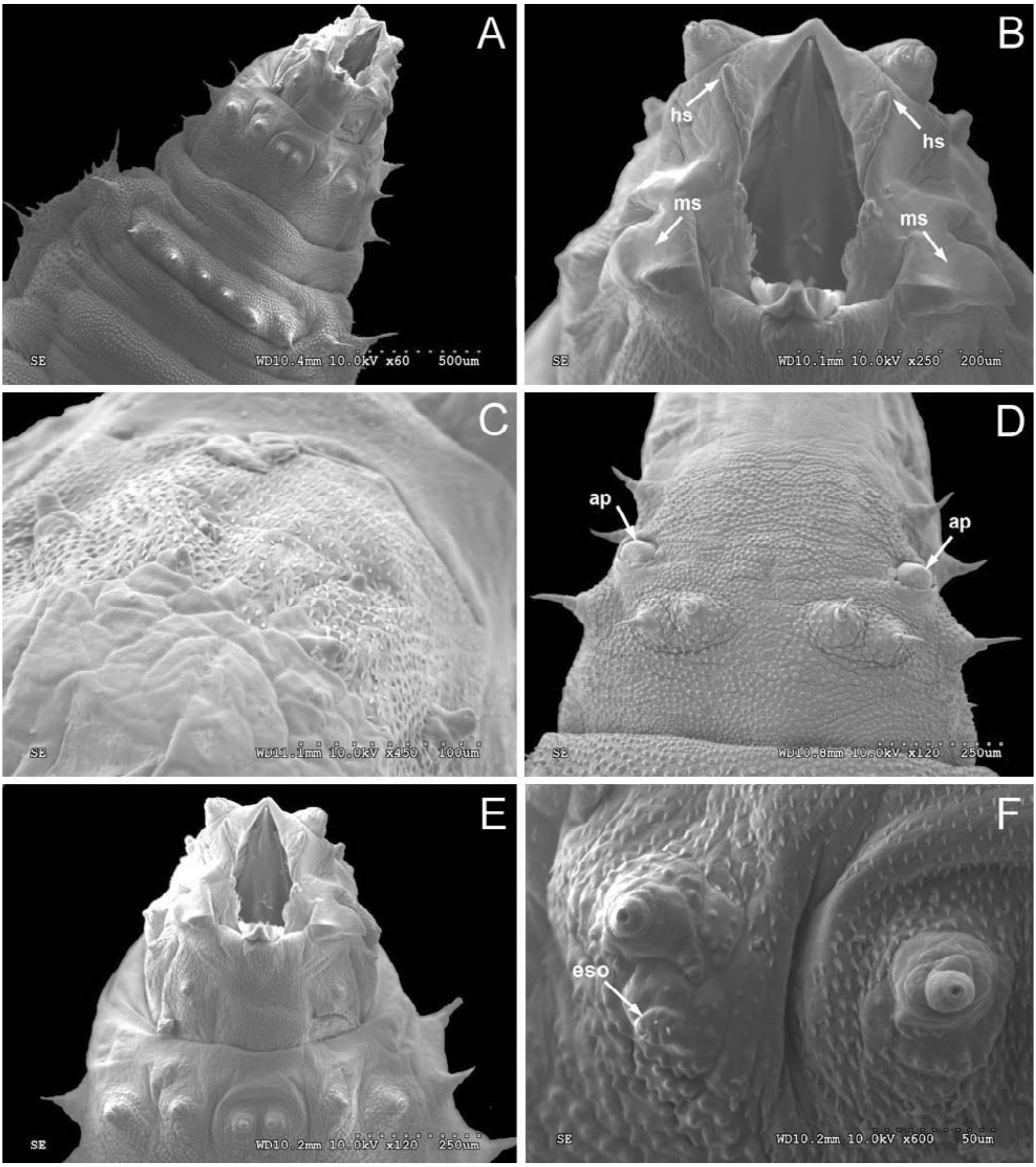

Fig. 2. Third instar larva of *Scaeva dignota*. A – head and thorax, ventral view; B – head, anteroventral view (ms – prothoracic sclerites, hs – head sensilla); C – dorsal surface of prothorax; D – mesothorax, dorsal view (ap – anterior respiratory process); E – prothorax and mesothorax, ventral view; F – detail of the extra pair of sensory-organ (eso) near sensillae 7^{Ms}, ventral view.

face covered with elongated microtrichia or rarely coated with short pointed, almost triangular spicules. PRP very short, only 0.15–0.25 mm long, without peritrema and normally recessed in a fleshy depression.

Head. Head very reduced (Fig. 2A). Mouthparts adapted for piercing-feeding (Hartley, 1963) with distinctive features of predacious syrphid larvae. Lateral margins of mouth with pair of black triangular pointed sclerites (Figs 2B, 3A). Antenno-maxillary organs well-developed (Fig. 2B). One pair of sensilla located above mouth and below antenno-maxillary organs (Fig. 2B).

Thorax. Prothorax with eleven pairs of sensillae hardly visible by light stereomicroscopy (Figs 2C, 4). Dorsal surface of prothorax with anterior respiratory process sclerotised and short, with semicircular openings on its anterior margin (Fig. 2D). Vestiture of prothorax above sensilla 4^{P} reduced, giving the integument a clear shining appearance (Fig. 2C). Anterior fold of prothorax with

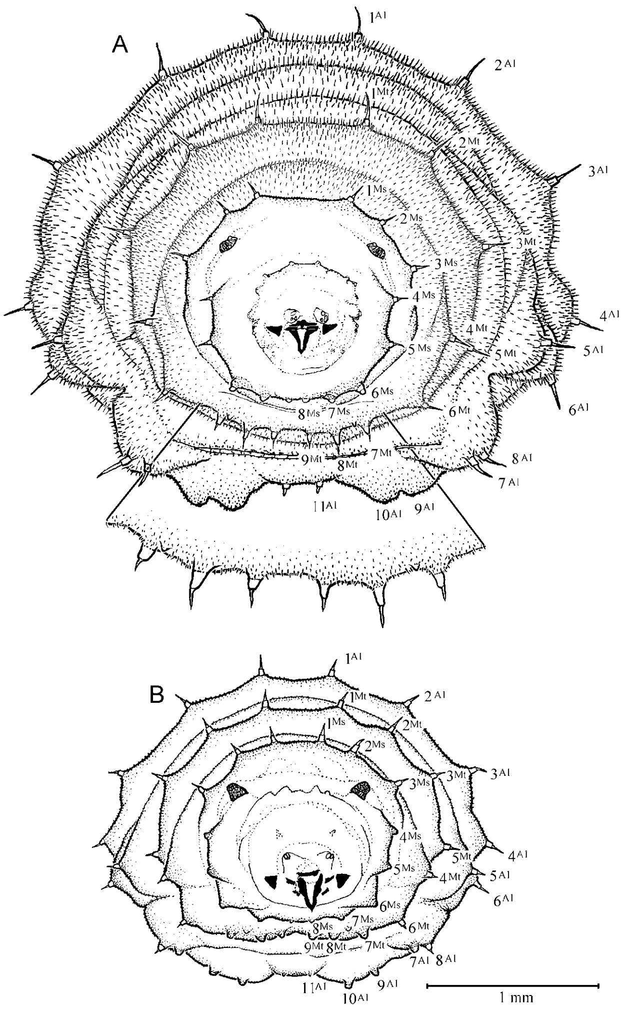

Fig. 3. Thoracic and first abdominal segments of the third instar larva, anterior view. A – *Scaeva selenitica* with two times magnified arrangement of 7^{Mt}–9^{Mt} segmental spines; B – *Syrphus ribesii*.

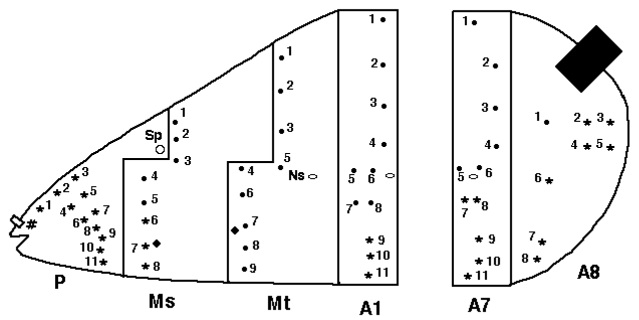

Fig. 4. Map of the chaetotaxy of the third instar larva of the *Scaeva* species showing the positions of the groups of sensillae: P – prothorax; Ms – mesothorax; Mt – metathorax; A1, A7 – first and seventh abdominal segments; A8 – eighth abdominal segment with PRP; Sp – anterior respiratory process; Ns – non-functional spiracle. Symbols: # – head sensillae; • – segmental spines; * – segmental sensillae without setae; ♦ – extra pair of sensory organs.

longitudinal grooves and a ring (extending < 35% of dorsal surface and < 60% of ventral surface) of small, backwardly directed spicules which become progressively densely-aggregated posteriorly on dorsal surface (Fig. 2C). Mesothorax with eight pairs of sensillae arranged in two main transverse rows: dorsal row with short segmental spines 1–3 and ventral row located slightly anteriorly bearing five pairs of sensillae, two pairs of dorso-lateral segmental spines followed by three pairs of ventral papiliform sensillae (Figs 2E, 3A, 4). Metathorax with nine pairs of sensillae arranged in two main transversal rows: dorsal row with four pairs of segmental spines and ventral row located slightly anteriorly with five pairs of segmental spines of unequal length; setae on sensillae 7^{Mt} and 9^{Mt} shorter than others (Figs 3A, 5A, 4). Contrary to e.g. *Syrphus* Fabricius, 1775, *Megasyrphus* Dušek et Láska, 1967 bearing on metathorax ventrally only papilliform sensillae (Fig. 3B). One extra pair of sensory-organs near sensillae 7^{Ms} and 7^{Mt} (hardly visible by light stereomicroscope) (Figs 2F, 5A).

Abdomen. Abdominal segments with eleven pairs of sensillae (Figs 3A, 4). First abdominal segment with three pairs of papiliform sensillae ventrally (Fig. 5B) and eight pairs of segmental spines dorso-laterally (Fig. 3A); pairs of segmental spines 1^{A1} and 2^{A1} located on the same fold. Second to seventh abdominal segments with the pair of segmental spines $1^{A2–7}$ on second fold and pair of segmental spines $2^{A2–7}$ placed on third fold, together with two further pairs of segmental spines. Five ventral pairs of sensillae reduced to papillae. On seventh abdominal segment, pair of segmental spines 1^{A7} separated from base of PRP by two folds, the posterior distinctly more developed (almost two times or more) and with microtrichia slightly enlarged in medial area. Integumental vestiture of the depression below PRP reduced in small nodules or spicules variable in their shape. On eighth abdominal segment, eight pairs of sensillae (Fig. 4), only first pair with setae (Figs 4, 5C). Locomotory prominences well developed; seven pairs present on abdominal segments 1–7 (Fig. 5B). Locomotory organs in front of anal openings consisting of four lobes each. Tip of anal segment with three pairs of lobes in ventral view (Figs 5C, 5D); posterior surface of lobes covered with densely-aggregated spicules, tip of lobes without vestiture (Fig. 5D). Anal papillae short, rudimental as in other Syrphini. One pair of papillae divided in two branches of identical length; length of papilla about 0.5–0.6 mm including common stem about 0.1–0.2 mm long, each branch cylindrical about 0.15–0.2 mm in diameter. **PRP**: Pale to dark brown in colour, lustrous. Spiracular plate differs at subgeneric level, divided by a V-shape median groove about as deep as half or more the length of PRP, dorsal spur present or absent (see Figs 6B, D). Orificia straight, mounted on well developed carinae extending towards side of PRP. Carinae about two times or more longer than broad. Periorificial ornamentation reduced, periorificial setae very small, hardly visible by light microscope, mounted inside of small circular nodules (Figs 6A, 6C).

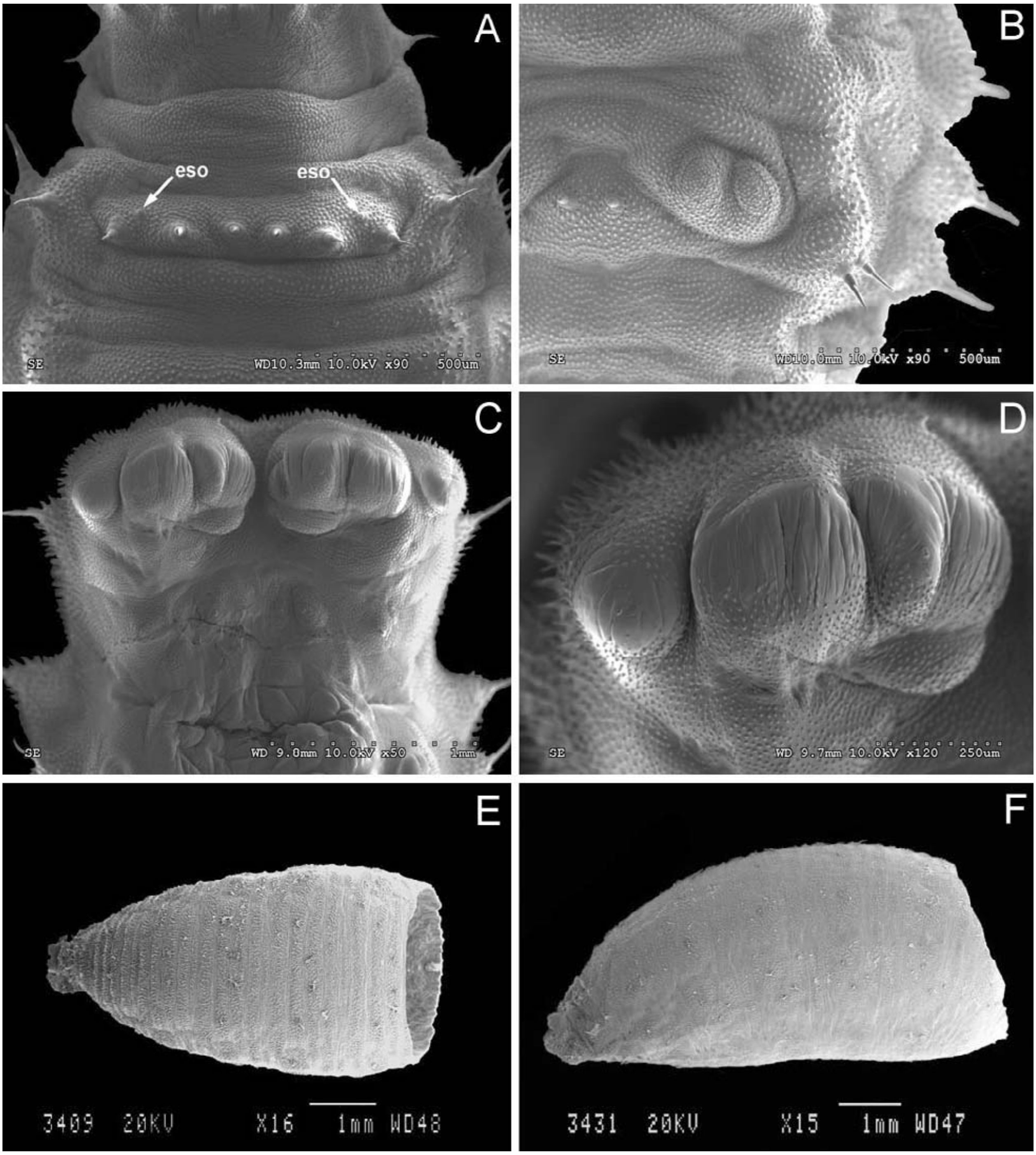

Fig. 5. *Scaeva dignota*. A – metathorax of third instar larva, detail of ventral chaetotaxy end extra pair of sensory organs (eso) near sensilla 7^{Mt}, ventral view; B – locomotory prominences of the first abdominal segment, ventral view; C – anal segment, ventral view; D – detail of locomotory organ on the tip of anal segment, ventral view; E – puparium, dorsal view; F – puparium, lateral view.

Puparium

Length 7.5–9 mm, maximum width 3.0–4.0 mm. Rather cask-like than pear-like, sub-cylindrical in cross-section (Fig. 5E). Anterior extreme truncated, slightly tapering posteriorly and flattened ventrally (Fig. 5F). Colour varies from cream to dull brown, sometimes with dark segmental patterns caused by pigmented cuticle. Dark patterns variable even at intraspecific level. Integumental vestiture and segmental spines persisting. Segmental spines of cuticle colour, about the same length as in larvae, but dried rests of fleshy projections bearing segmental spines usually inconspicuous. Sclerotised PRP almost without changes, only carinae black edging (Fig. 6).

Subgenus *Semiscaeva* Kuznetzov, 1985

Diagnostic characters. Colour pattern of larva variable in ground colour at intraspecific level (green, brown or pink) with a median dorsal white, cream or pink stripe.

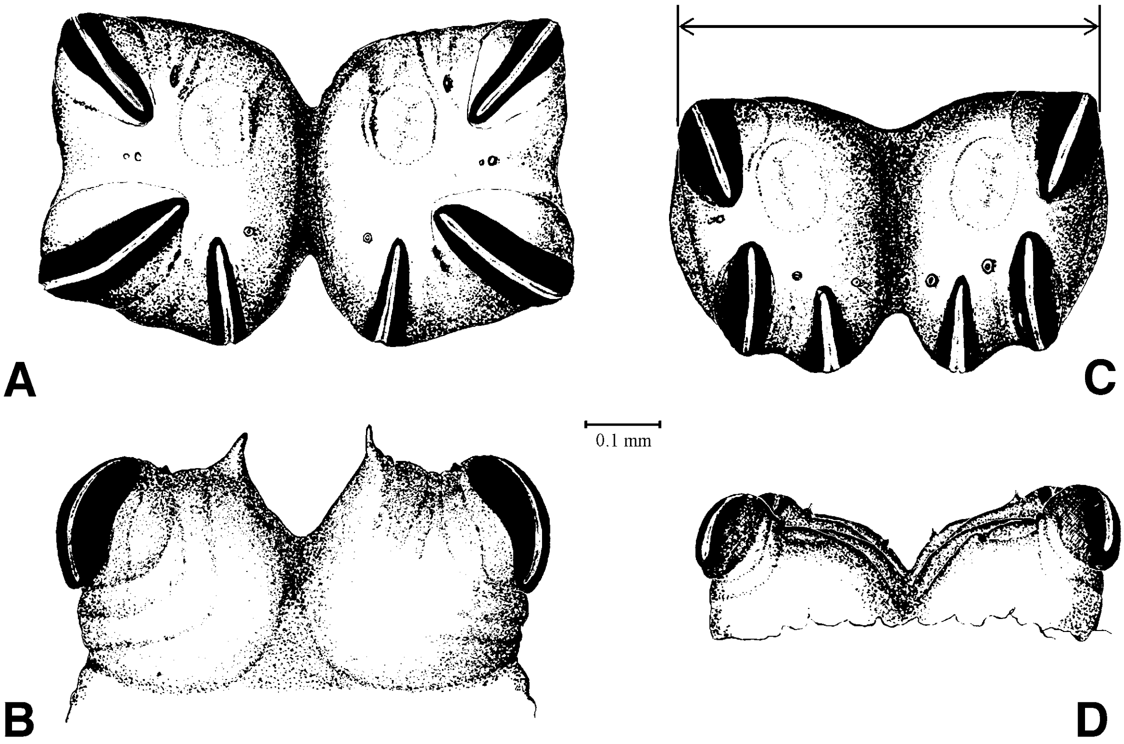

Fig. 6. PRP of puparium of *Scaeva* spp. (A, C – posterodorsal view; B, D – anterodorsal view). A, B – *S.* (*Semiscaeva*) *selenitica*; C, D – *S.* (*Scaeva*) *pyrastri* (measurement of the width of the PRP marked).

Integument coated with distinct, not furcate microtrichia about 0.03–0.07 mm long on dorsum; posterior folds coated with microtrichia with wide base and narrow tip (Figs 7A, 7C, 7E); integument of depression below PRP covered with smaller, scarcer, pedunculate nodules and spicules (Figs 7B, 7D, 7F). **PRP**: Short (0.19–0.29 mm long), pale to dark brown in colour. Spiracular plate as high as wide, or a little higher than wide (Fig. 6A). V-shaped median grove about as deep as half the length of PRP (Fig. 6B). Dorsal spur present, short (about 0.02–0.03 mm long), pointed and continuous with medial border of ecdysial scar (Figs 6A, 6B). Orificia equidistant from each other; angle between orificia I/II and II/III near 90° (Fig. 6A). Orificia mounted on raised carinae and all extending more than 0.5 of their length down the sides of PRP (Fig. 6B). Carinae I and II a little more developed than carina III.

Scaeva selenitica (Meigen, 1822)

Immature stages previously described by Scott (1939), Brauns (1953), Dušek & Láska (1959), Dixon (1960) and Speight et al. (1986, only puparium). Larvae predatory on a wide range of aphids, prey records cited by Rojo et al. (2003, p. 202–204).

Diagnostic characters. The larva can present two patterns of colouration, green with a white median stripe (as in *S. pyrastri*) or brownish similar to *Eupeodes* spp. larvae. Body surface coated with well developed brown pigmented microtrichia about 0.03–0.045 mm long on dorsum. Dark segmental pattern on puparium present as dots arranged on dorsum, even if sometimes inconspicuous. Posterior folds coated with microtrichia with a wide base that becomes suddenly fine (Fig. 7A). **PRP**: (Width: 0.56–0.65 mm, height: 0.30–0.41 mm, n = 10). Short, pale brown in colour. Median groove deeper than half the length of PRP, in anterior view tips of dorsal spurs as wide apart as more than semi-diameter of spiracular plate (Figs 8A, 8B). Ecdysial scars displaced towards median groove and anteriorly (Fig. 8A). Carinae I and II well developed with clear depression between them (Fig. 8A). Periorificial setae mounted inside of circular nodules, periorificial setae between orificia I and II close, with their nodules connected (Fig. 8A).

Material examined. Czech Republic. Olomouc – Svatý Kopeček: about 30 puparia, reared from eggs, female 24.viii.1974, leg. P. Láska; Valy u Přelouče: 4 puparia (3♀, 1♂) 4 larvae, reared from eggs, female 29.v.1999, leg. L. Mazánek; Ostrava, Polanecký les: 11 puparia (6♂, 5♀) 13 larvae, reared from eggs, female 3.iv.2000, leg. T. Kuras; Lestkov, Distr. Chomutov: 9 puparia, 19 lyophilised larvae, reared from eggs, female 21.iv.2000, leg. L. Mazánek.

Distribution. Palaearctic, subboreal (see also discussion).

Scaeva mecogramma (Bigot, 1860)

Immature stages described here for the first time. Rojo et al. (1999) studied larval biology and two species of psyllids on olive-trees were cited as prey. Larvae are probably specialised predators of psyllids.

Diagnostic characters. Only green larvae with white medial stripe were observed. Body of larvae and puparia usually totally covered with whitish waxen flakes secreted by psyllids. Microtrichia of cuticle colour, well developed, about 0.04–0.07 mm long on dorsum. Cuticle of puparium without dark patterns. **PRP**: (Width:

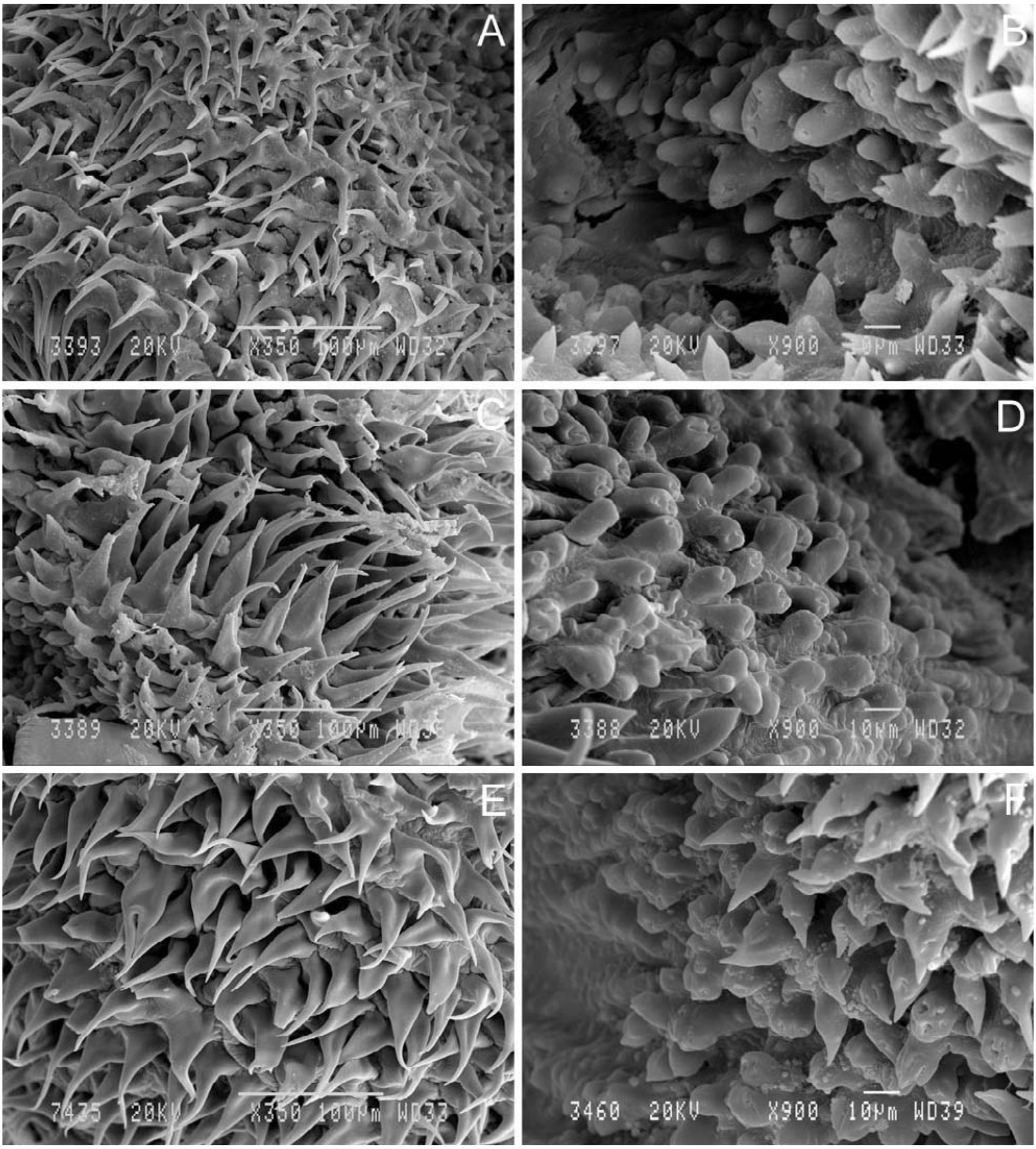

Fig. 7. Puparium of *Scaeva* (*Semiscaeva*) spp. (A, C, E – microtrichia on the central area of the posterior fold, dorsal view; B, D, F – integumental vestiture of the depression below PRP). A, B – *S. selenitica*; C, D – *S. mecogramma*; E, F – *S. dignota*.

0.35–0.4 mm, height: 0.20–0.25 mm, n = 6). PRP smaller and darker in relation to *S. selenitica/dignota*. Short and dark brown in colour at least in puparium. Median groove slightly less deep than half the length of PRP, tips of the dorsal spurs as wide apart as less than semi-diameter of spiracular plate (Figs 8C, 8D). Ecdysial scars displaced towards median groove and anteriorly (Fig. 8C). Periorificial setae mounted inside of circular nodules, periorificial setae between orificia I and II close, but border of their nodules separated (Fig. 8C).

Material examined. Spain. Valencia, Moncada: 4 puparia (1♂, 3♀) leg. as larvae 23.xi.1996, leg. M.J. Verdú; 3 puparia (2♂, 1♀) leg. as larvae 18.vii.1996, leg. M.A. Marcos-García; 1 puparium (♂) 8 larvae, leg. as larvae 23.xii.1996, leg. S. Rojo; Alicante, San Vicente del Raspeig: 3 larvae, leg. as larvae 13.v.1998, leg. J.V. Falcó; 3 puparia (1♂, 2♀) leg. as larvae 7.vi.1998, leg. J.V. Falcó.

Distribution. South Europe.

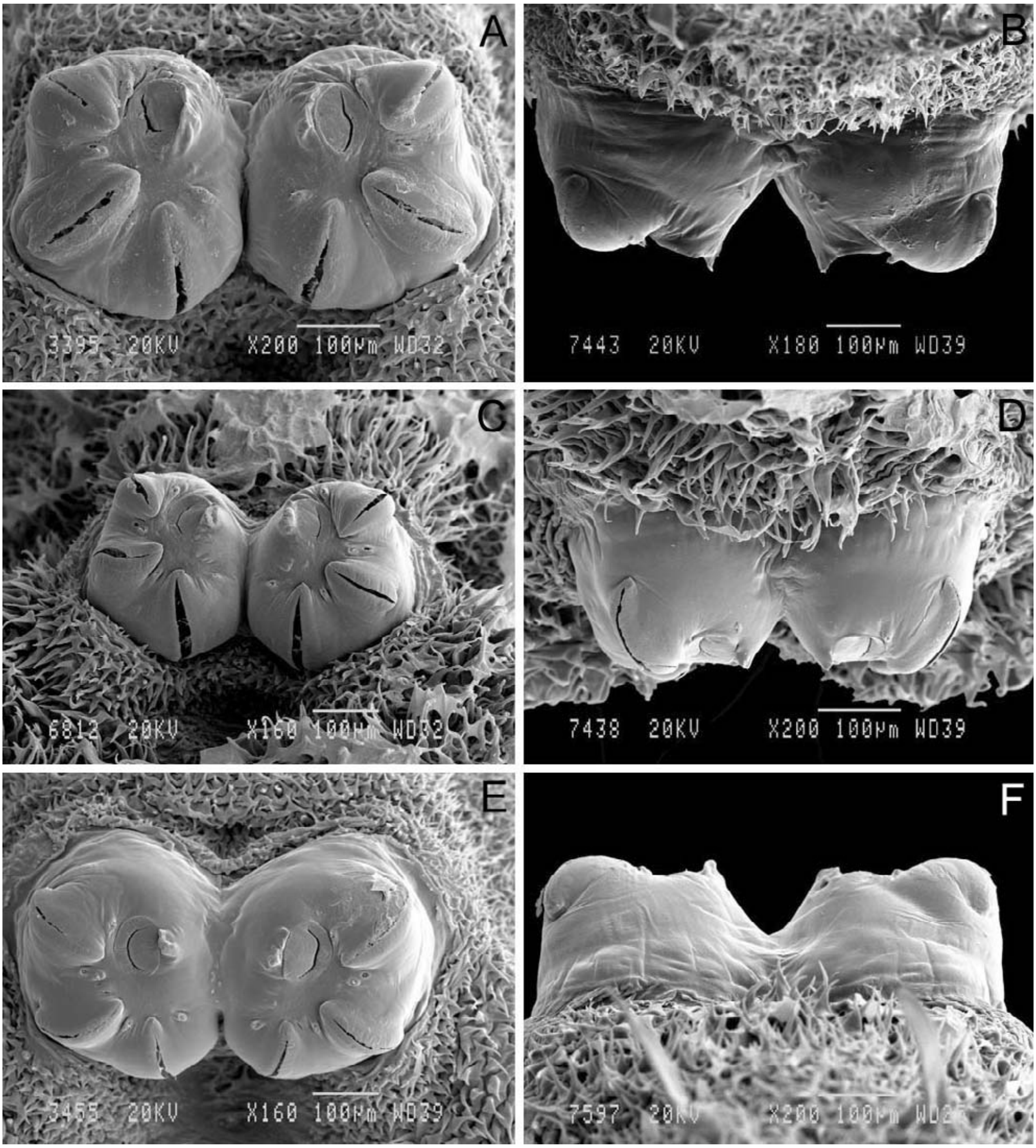

Fig. 8. PRP of puparium of *Scaeva* (*Semiscaeva*) spp. (A, C, E – posterodorsal view view; B, D, F – anterodorsal view). A, B – *S. selenitica*; C, D – *S. mecogramma*; E–F – *S. dignota*.

Scaeva dignota **(Rondani, 1857)**

Immature stages described here for the first time. Larvae probably predatory on a wide range of aphids. Prey records cited by Dušek & Láska (1985) and Starý & Havelka (1991). Prey records from southern part of Europe could be erroneously referred to *S. selenitica*.

Diagnostic characters. Larva and puparium very similar to *S. selenitica* including coloration variability of larvae. Dorsal body surface coated with well developed microtrichia about 0.03–0.045 mm long, pigmentation of microtrichia less intense than in *S. selenitica*, cuticle of puparium mainly without dark segmental patterns. Posterior folds coated with microtrichia with a wide base that become progressively fine (Fig. 7E). **PRP**: (Width: 0.45–0.55 mm, height: 0.28–0.36 mm, n = 30; PRP size not affected by parasitation of *Diplazon* Ness, 1818 (Hymenoptera: Ichneumonidae), contrary to the observation of Dušek et al. (1979), who described the influence of parasitation on PRP size of puparia in *Syrphus*). Median groove deeper than half the length of PRP, in

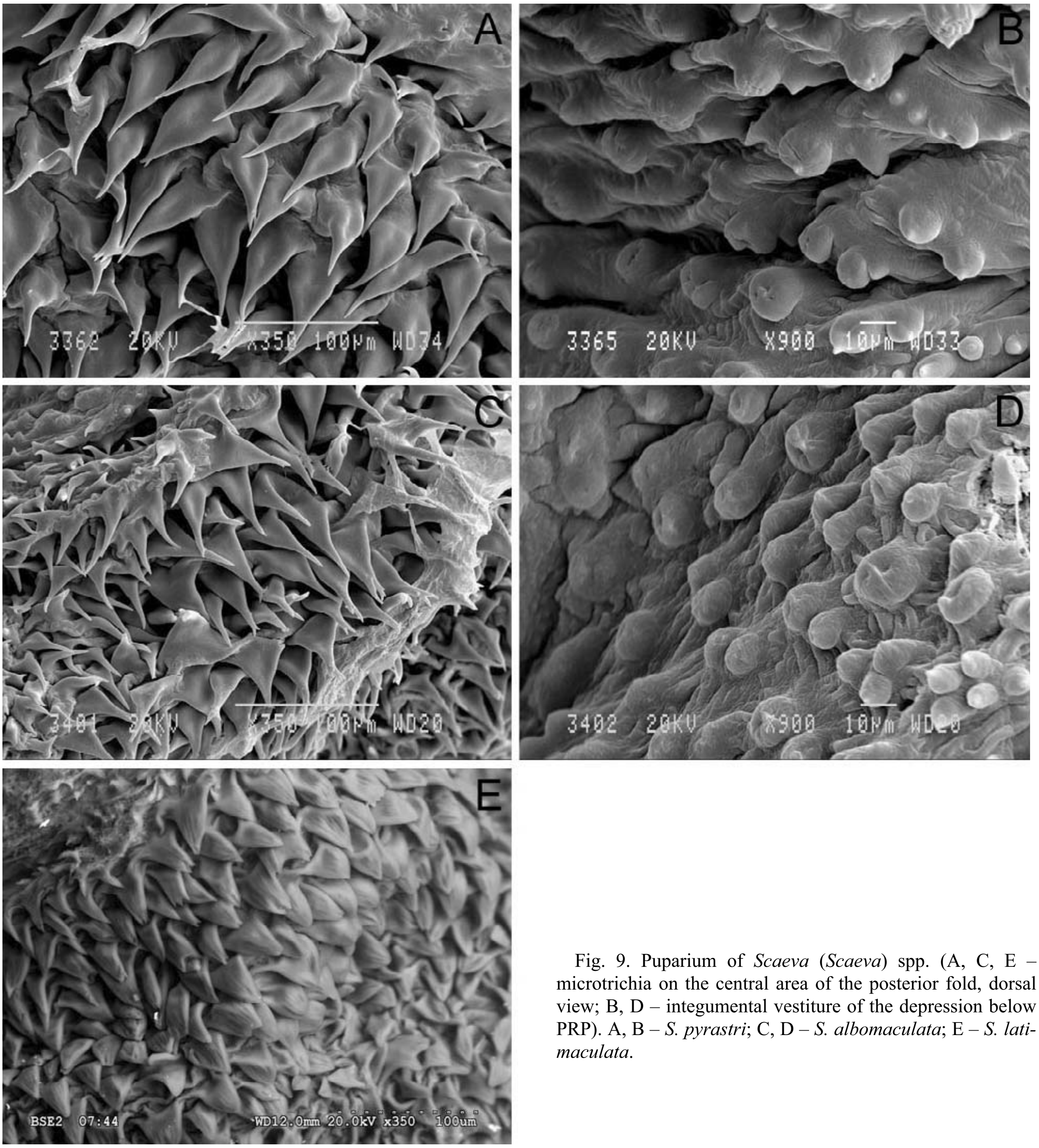

Fig. 9. Puparium of *Scaeva* (*Scaeva*) spp. (A, C, E – microtrichia on the central area of the posterior fold, dorsal view; B, D – integumental vestiture of the depression below PRP). A, B – *S. pyrastri*; C, D – *S. albomaculata*; E – *S. latimaculata*.

anterior view tips of dorsal spurs as wide apart as more than semi-diameter of a spiracular plate (Figs 8E, F). Ecdysial scars slightly anterior to centre of each spiracular plate (Fig. 8E). Periorificial setae mounted inside of circular nodules, periorificial setae between orificia I and II close, but border of their nodules separated (Fig. 8E).

Material examined. Czech Republic. Žlunice, distr. Jičín: 1 puparium (♂ numbered G 72), leg. as puparium 23.vi.1959 on the blade of grass in deciduous forest, leg. P. Láska; Olomouc: 1 puparium (♀ numbered 5VZ01/1), leg. as larva 21.vi.2001 feeding on *Aphis sambuci* on *Sambucus nigra*, leg. M. Štibnarová & M. Hanáková; 1 puparium (♀), leg. as larva 10.vi.1994, leg. L. Mazánek. Turkey. İzmir, Karşiyaka: 1 puparium, leg. as larva 19.iv.1976 on aphids colony on *Prunus domestica*, leg. E. Erkin; İzmir, Urla: 1 dried larva, 24.iv.1975 on aphis colony on *Vicia faba*, leg. E. Erkin; İzmir, Menemen: 1 puparium, leg. as larva 21.iv.1975 on aphis colony on *Prunus communis*, leg. E. Erkin. Greece. Lesbos, Mytilene: 3 puparia (1♂, 2♀) leg. as larvae 10.iii.2001, leg. S. Rojo & C. Pérez-Bañón; Polihnitos: 9 puparia (4♂, 5♀) leg. as larvae, leg. S. Rojo & C. Pérez-Bañón; Agh. Paraskevi: 10 puparia (6♂, 4♀) leg. as larvae 27.iii.2001, leg. S. Rojo & C. Pérez-Bañón. Spain. Alicante. Tibi: 7 puparia (4♂, 2♀) leg. as larvae 21.v.1993; leg. S. Rojo; Villena: 3 puparia (3♀) leg. as larvae 16.iv.1993; leg. S. Rojo; Biar: 2 puparia (2♀) leg. as larvae 16.iv.1993; leg. S. Rojo.

Distribution. Sub-Mediterranean (see also discussion).

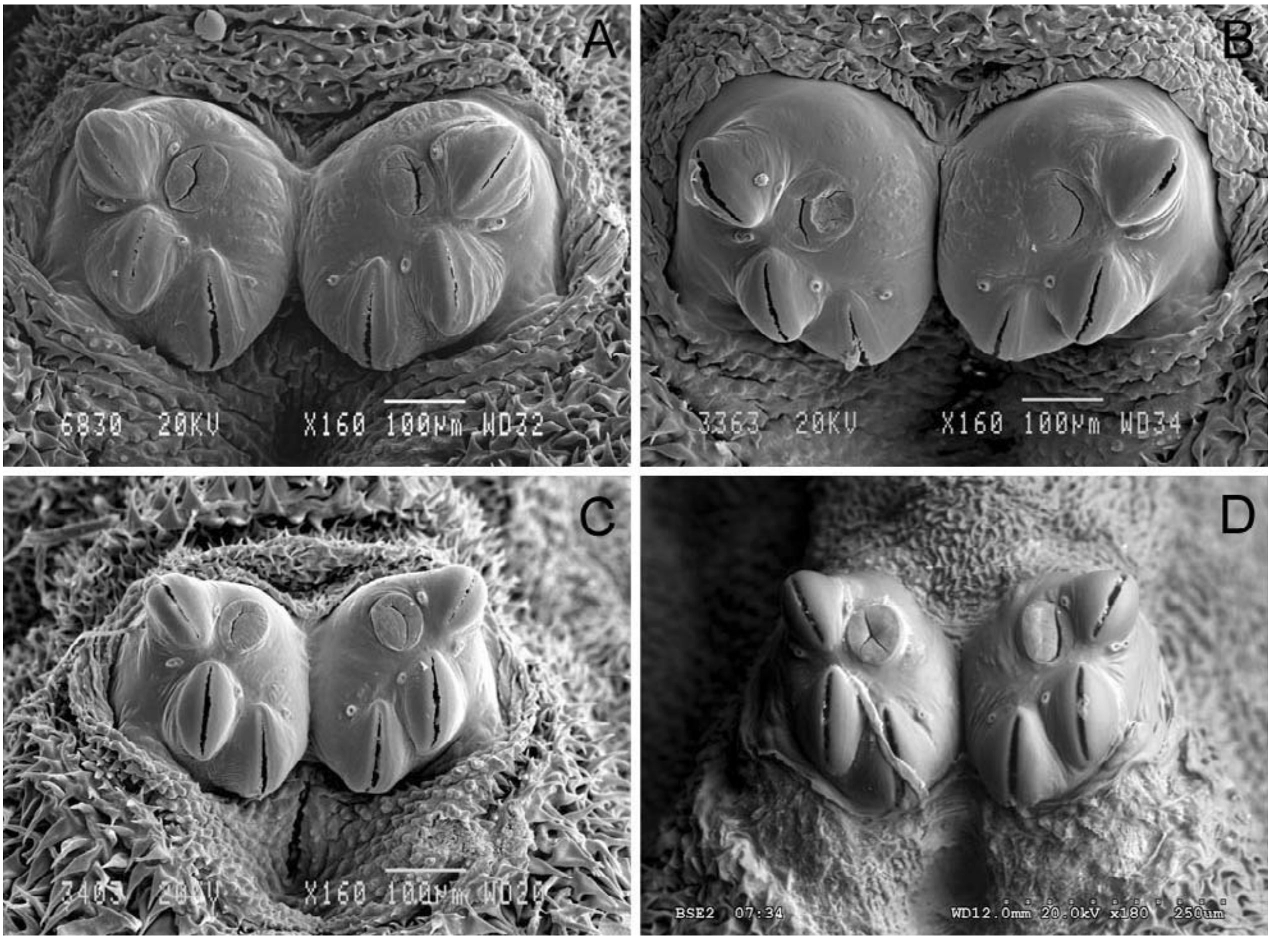

Fig. 10. PRP of puparium of *Scaeva* (*Scaeva*) spp., posterodorsal view; A, B – *S. pyrastri*; C – *S. albomaculata*; D – *S. latimaculata*.

Subgenus *Scaeva* s. str.

Diagnostic characters. Colour pattern of larva constant, green with white median dorsal stripe. Rarely with pink shade and ochre dorsal stripe. Integument coated with microtrichia, about 0.02–0.035 mm long on dorsum, that could be reduced to short, almost triangular spicules; microtrichia of cuticle colour or brown pigmented, often furcate especially on folds around PRP. Integument of the depression below PRP covered with smaller, scarcer, slightly pedunculate nodules (Figs 9B, 9D) of whitish colour in puparium. **PRP**: very short, almost sessile (0.12–0.15 mm long), pale to dark brown in colour. Spiracular plates divided by a V-shape median groove almost as deep as the length of PRP (Fig. 6D). Dorsal spur absent; orificia II and III parallel, orificium III inserted on about 1/3 to nearly 1/2 of length of orificium II posteriorly than orificium II; carinae I and III extending down the sides of PRP; carinae I and II distinctly more developed than carina III (Fig. 6C). Periorificial setae mounted inside of circular nodules; periorificial setae between orificia I and II very close, with border of their nodules connected (Fig. 6C).

***Scaeva pyrastri* (Linnaeus, 1758)**

Previously described by Martelli (1911), Jones (1922), Krüger (1926), Fluke (1929), Heiss (1938), Bhatia (1939), Scott (1939), Brauns (1953), Láska (1959), Dušek & Láska (1959), Dixon (1960), Goeldlin de Tiefenau (1974). Sharma & Bhalla (1988) dealt with larval biology on laboratory breeding but did not describe immature stages. Barkemeyer (1994) provides a comprehensive literature review of what is known on the biology of this species. Larvae are predatory on a wide range of aphids and also Coccidae, Psyllidae and Thysanoptera; prey records listed by Rojo et al. (2003, p. 192–202).

Diagnostic characters. The last fold anteriorly on PRP rounded, without conical fleshy projection at median point. Segmental spines well developed, about 0.15–0.25 mm long similar as in the other *Scaeva* species. Integument on dorsum covered with distinct microtrichia about 0.02–0.035 mm long, of cuticle colour, some of them furcate around PRP. Posterior folds coated with microtrichia with a wide base that becomes progressively fine to apex (Fig. 9A). Puparium usually without brown cuticle segmental patterns and without dried fleshy projections under segmental spines. **PRP**: (width: 0.5–0.59 mm, height: 0.28–0.36; n = 10). Almost sessile, lustrous, sclerotized and pale brown in colour. Ecdysial scars slightly anterior to centre of each spiracular plate. Orificia I and II aligned or with angle between them a little less than 180°; orificia II and III almost parallel (Figs 10A, B).

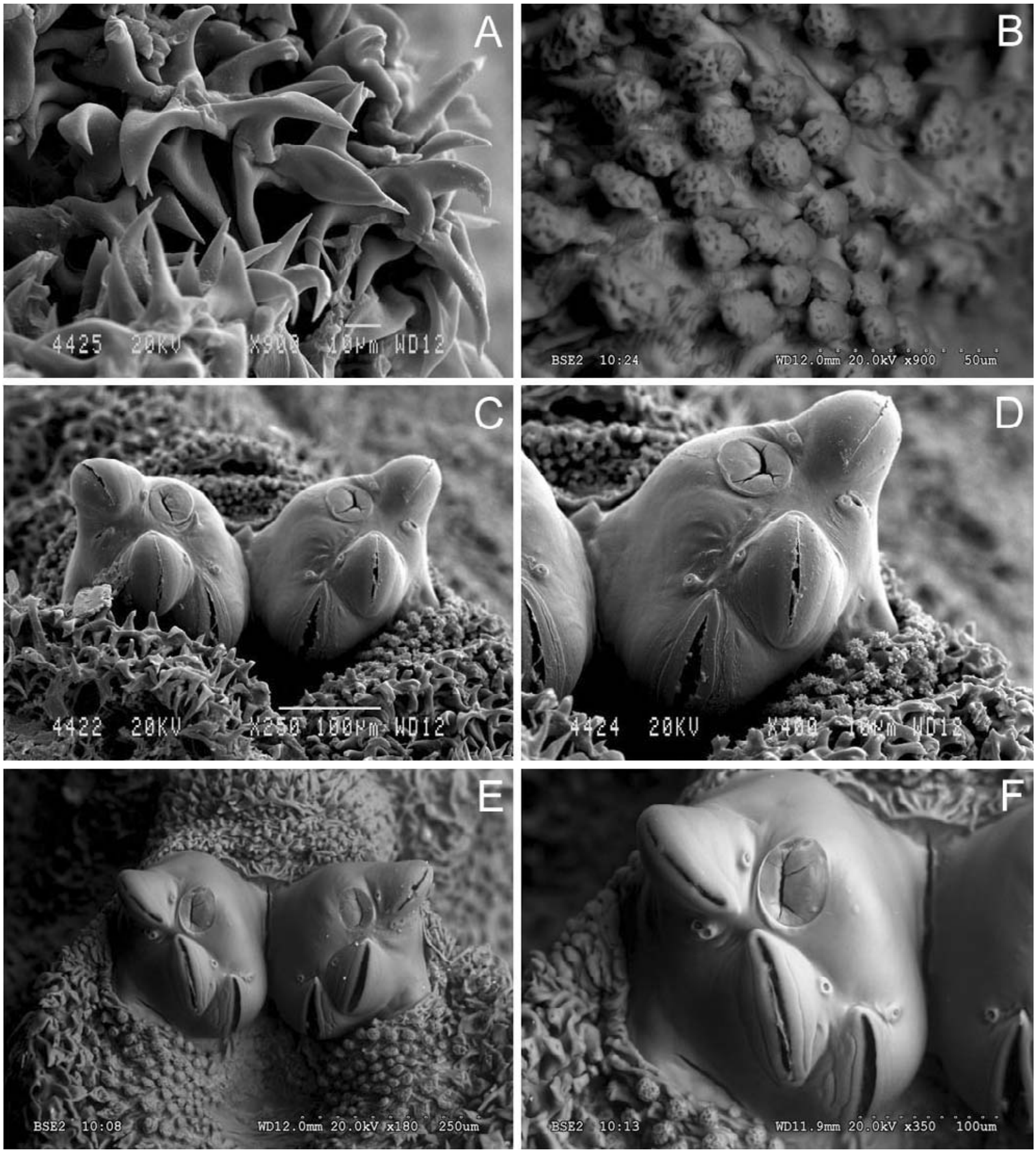

Fig. 11. Puparium of *Simosyrphus* s. l. A–D – *S. aegyptius*: A – microtrichia on the central area of the posterior fold, dorsal view; B – integumental vestiture of the depression below PRP; C – PRP, posterodorsal view; D – spiracular plate, posterodorsal view. E, F – *S. grandicornis*: E – PRP, posterodorsal view; F – spiracular plate, posterodorsal view.

Material examined. Montenegro. Bečiči near Budva: 9 puparia, leg. as larvae v.1968 feeding on *Uroleucon cichorii* on *Cichorium intybus*, leg. P. Láska. Czech Republic. Olomouc: 1 puparium (♂) leg. as larva on aphid colony on *Cirsium arvense*, 10.vi.1999, leg. L. Mazánek; 53 puparia (24♂, 29♀) 5 lyophilised larvae, 4 larvae in alcohol, reared from eggs, female 14.vi.2001, leg. L. Mazánek; 2 puparia (♂) 1 larva, leg. as larvae 4.vii.2003 feeding on *Uroleucon cichorii* on *Cichorium intybus*, leg. L. Mazánek; Mikulčin vrch: 1 puparium (♀) leg. as larva feeding on *Uroleucon cichorii* on *Cichorium intybus*, 8.ix.2000, leg. L. Mazánek. Greece. Lesbos, Agh. Parakevi: 1 puparium (♀) leg. as larvae 27.iii.2001, leg. S. Rojo & C. Pérez-Bañón; Mistegna: 1 puparium (♀) leg. as larvae 17.iv.2001, leg. S. Rojo & C. Pérez-Bañón; Mandamados: 1 puparium (♂) leg. as larvae 18.v.2001, leg. S. Rojo & C. Pérez-Bañón. Spain. Alicante, San Vicente del Raspeig: 2 puparia (2♀) leg. as larvae 13.iii.2000, leg, E.S. Ráez; San Vicente del Raspeig: 1 puparium (♀) leg. as larvae 21.iii.2000, leg, E.S. Ráez; San Vicente del Raspeig: 1 puparium (♂) leg. as larvae 28.iii.2000, leg, E.S. Ráez; San Vicente del Raspeig: 1 puparium (♀) leg. as larvae 17.xi.2000, leg, E.S. Ráez.

Distribution. Holarctic and marginally Oriental region.

Scaeva albomaculata (Macquart, 1842)

Previously described by Kuznetzov & Daminova (1994). Larvae predatory on a wide range of aphids; prey records listed by Rojo et al. (2003, pp. 190–192).

Diagnostic characters. Last fold anterior of PRP enlarged, forming conical fleshy projection at median point (Fig. 1C). Fully developed segmental spines about 0.15–0.25 mm long. Integument on dorsum covered with distinct microtrichia about 0.02–0.035 mm long, browned towards top and often furcate on folds around PRP. Posterior folds coated with microtrichia with a wide base becoming progressively fine to apex (Fig. 9C). Puparium usually with tubercle (= rest of dried fleshy conical projection in larva) before PRP (Fig. 1D) and also dried fleshy projection often persist as microtrichose portion under base of some segmental spines on posterior part of puparium. **PRP**: (width: 0.39–0.44 mm, height: 0.25–0.3, n = 5). Almost sessile, lustrous, sclerotized and pale brown in colour. Ecdysial scars displaced towards the median groove and anteriorly; orificia II and III almost parallel (Fig. 10C).

Material examined. Spain. Alicante, San Vicente del Raspeig: 1 lyophilised larva, reared from eggs, female 27.ii.2000, leg. L. Mazánek; Ibi: 6 puparia (4♂, 2♀) leg. as larvae 6.vii.1992, leg. S. Rojo; Villena: 3 puparia (2♂, 1♀) leg. as larvae 26.vi.1992, leg. S. Rojo; Sax: 1 puparium (♂) leg. as larva 28.vi.1992, leg. S. Rojo; Alcoy: 1 puparium (♀) leg. as larva 21.v.1992, leg. S. Rojo. Italy. Roma, park Glyphinia: 1 puparium (numbered 63/307), leg. as larva 16.vi.1963, leg. P. Starý.

Distribution. South part of Palaearctic to north part of Oriental region.

Scaeva latimaculata (Brunetti, 1923)

Previously described by Kumar et al. (1987). Several economically important aphid species were cited as prey of this species by Agarwala et al. (1984) and Kumar et al. (1987).

Diagnostic characters. The larva is similar to that of *S. pyrastri*, from which it differs by less developed integumental vestiture, microtichia reduced to short, almost triangular spicules not longer than 0.02 mm, spicules of cuticle colour or browned. Segmental spine shorter than in the other *Scaeva* species; most developed spines about 0.15 mm long. Posterior folds coated with longer microtrichia not fine at apex and often furcate (Fig. 9E). Cuticle of puparium with or without darkened segmental patterns, rests of dried fleshy projections absent. **PRP**: (width: 0.33–0.39 mm, height: 0.21–0.26 mm, *n* = 2). Ecdysial scars displaced towards the median groove and anteriorly; orificium I on most developed carina that overlaps anterior margin of spiracular plate in dorsal view; orificia II and III almost parallel (Fig. 10D).

Material examined. India. Punjab: 1 puparium (♀ – SEM photos). leg. as larva, leg. A. Kumar; Himachal Pradesh, 1 puparium (♀ numbered 104), leg. as larva on *Hyperomyzus carduellinus* on *Emilia sonchi* leg. K. Agarwala. Iran. Mahabad 82 km S., 2600 m: 1 puparium (♀) leg. as larva 6.vii.1974 on *Papaver* sp., leg. C. Buckingham.

Distribution. Southern Palaearctic from Iran eastwards into Oriental region.

Simosyrphus Bigot, 1882

Third instar larva

We could not examine the larvae, but according to previous descriptions of Barbosa (1952), Lal & Gupta (1953), Tawfik et al. (1974), Roy & Basu (1977), Kumar et al. (1987), Soleyman-Nezhadiyan (pers. com.) and a black and white photo of Schmutterer (1972), the larvae of this genus are very similar to smaller larvae of *Scaeva* s.str. in overall appearance: (Length including PRP 7–12.5 mm, maximum width 2–3 mm) oval in cross-section, relatively high; locomotory prominences well developed; body wrinkled and green coloured with mid-dorsal whitish stripe. Some species have on each side of white stripe a line of spots or narrow stripes orange to light brown coloured and spots or stripes along lateral margins of larvae. These patterns also visible in fleshy projection bearing segmental spines. However, Rotheray & Gilbert (1999) give some new characters that show the close relation between these two genera: presence of setae on the sensillae 7^{Mt}, 8^{Mt} and 9^{Mt} (that was confirmed by our study of puparia); the locomotory prominences on 6th and 7th abdominal segments with the tips directed backwards; and an extra lobe on the locomotory prominences of abdominal segments 1–7.

We can add some new data to this list of characters obtained from the puparium: segmental spines relatively long (about 0.1–0.21 mm long in dorsum, measured in puparium), with the same pattern and arrangement as in the *Scaeva* species, only fleshy projections bearing segmental spines are more developed. Integument covered by short pointed spicules rather than microtrichia, about 0.02 mm long, on posterior folds longer and wider and often furcate (Fig. 11A); integument of depression below PRP and also small area close before PRP covered with nodular rounded papillae (Fig. 11B).

PRP: similar to PRP of sg. *Scaeva*, very short, almost sessile (0.1–0.15 mm long), only width of PRP differs according to species. Spiracular plates higher than wide, divided by a V-shape groove as deep as length of PRP; dorsal spur absent; orificia II and III almost parallel; orificium III inserted more posteriorly than in the *Scaeva* subgenus, on about half or more of the length of orificium II. Carina I well developed, distinctly overlapping the anterior margin of spiracular plate in dorsal view (Figs 11C–F). Periorificial ornamentation reduced as in the *Scaeva* species; periorificial setae very small hardly visible by light microscope, mounted inside of small circular nodules (Figs 11C–F); periorificial setae between orificia I and II very close, with border of their nodules connected.

Puparium

Length including PRP 5.5–7.0 mm, maximum width 2.5–3.2 mm. Puparia of similar shape as in *Scaeva* but smaller. Colour varying from cream to dull brown, also at intraspecific level. Integumental vestiture persisting, of cuticle colour or a little darkened, rarely forming slightly darkened segmental patterns with pigmented cuticle. Segmental spines elongated by persisting dried fleshy projections that form microtrichose portion under segmental spines, especially on dorsum of posterior part of puparium. Segmental spines of cuticle colour or browner, variable also at intraspecific level. PRP with carinae usually blacked, nodular integument of depression below PRP and also small area close before PRP usually whitish.

Simosyrphus grandicornis (Macquart, 1842)

Soleyman-Nezhadiyan (1997) and Soleyman-Nezhadiyan & Laughlin (1998) deal with larval biology of laboratory breedings but do not describe immature stages. Larvae predatory on a wide range of aphids and even lepidopteran larvae; prey records reported by Rojo et al. (2003, pp. 204–205).

Diagnostic characters. Larva green with whitish median stripe (E. Soleyman-Nezhadiyan, pers. com.). Segmental spines relatively short, fully developed only about 0.1–0.14 mm long, fleshy projections bearing segmental spines less developed, dried persist under several segmental spines on posterior part of dorsum of puparium as microtrichose portion (maximum length 0.05 mm). Microtrichia of cuticle colour or slightly dark brown pigmented, especially around segmental spines, but puparium without visible dark coloured pattern. **PRP**: somewhat smaller than in other species of the genus, about 0.26–0.30 mm wide and 0.14–0.18 mm high (n = 2). Length of PRP about 0.1 mm. Carina I well developed, rounded apically (Fig. 11D).

Material examined. Australia. Nethy Bridghe: 1 puparium (♀) leg. as larva 11.xi.1974; 1 puparium (♀ – SEM photos), reared on *Hyperomyzus lachicae*, leg. as larva 11.xi.1974; Mosman NSU: 1 puparium (♂) reared on *Schaitedonia lutea*, leg. as larva 18.i.1973. All leg. D. Hales.

Distribution. Australia, Oceania.

Simosyrphus aegyptius (Wiedemann, 1830) comb. n.

Previously described by Barbosa (1952), Tawfik et al. (1974). Larvae predatory on a wide range of aphids and also on Thysanoptera; prey records cited by Rojo et al. (2003, p. 116–118). Even lepidopterous larvae were cited as preys by Randrianandrianina-Razananaivo (1991).

Diagnostic characters. Larva yellowish green with mid-dorsal white stripe flanked by developing narrow orange or light brown stripes; yellowish orange fat bodies discerned also in fleshy projections forming lateral orange line. As the fat bodies extend, larvae become rather yellowish orange. Fully developed segmental spines about 0.16–0.2 mm long mounted on well developed fleshy projection that dried persist on puparium under segmental spines as microtrichose portion long almost 0.12 mm, especially on posterior part of dorsum. **PRP**: about 0.38–0.43 mm wide and 0.24–0.30 mm high (n = 5). PRP length about 0.12–0.14 mm. Carina I rather sharp apically (Fig. 11F).

Material examined. Kenya. Nairobi-Chiromo: 4 puparia (2♂, 2♀) reared on *Rhopalosiphum maidis*, leg. as larvae 22.ii.1970, leg. H. Schmutterer; 2 puparia (♀) reared on *Rhopalosiphum maidis*, leg. as larvae 20.vi.1970, leg. H. Schmutterer. Senegal. Ziguinchor, Djibélor: 3 puparia (2♂ – SEM photos, 1♀) leg. as larvae 18.xi.1979 on *Toxoptera aurantii*, leg. J. Etienne.

Distribution. Afrotropical, including Madagascar, Réunion and South-West Palaearctic (North Africa, Southern Spain, Madeira and Canary Islands).

Simosyrphus scutellaris (Fabricius, 1805) comb. n.

Immature stages were previously described by Lal & Gupta (1953), Okuno (1967), Roy & Basu (1977) and Kumar et al. (1987). Ninomyia (1959) described only the puparium of an aberrant specimen with only two orificia on one of two spiracular plates. Lal & Haque (1965), Agarwala & Saha (1986), Sharma & Bhalla (1988) and Singh & Mishra (1988) studied biology of immature stages in detail but did not describe the immature stages. Larvae predatory on a wide range of aphids and even lepidoptera larvae; prey records listed by Rojo et al. (2003, p. 118–122).

Diagnostic characters. Larvae green to greenish-brown coloured with mid-dorsal whitish stripe and with reddish to brown fat bodies along mid-dorsal stripe, in fleshy projections and along lateral margin of larvae. Fully developed segmental spines about 0.13–0.18 mm, mounted on well developed fleshy projection that dried persist on puparium under base of segmental spines as microtrichose portion long almost 0.08 mm, especially on posterior part of dorsum. **PRP**: about 0.43–0.53 mm wide and 0.26–0.34 mm high, (n = 2); length about 0.13 mm.

Material examined. India. Punjab: 1 puparium (♂) leg. as larva, leg. A. Kumar; Agartala: 1 puparium, leg. as larva 1980 on *Aphis gossypii* on *Gossypium* sp., leg. K. Agarwala.

Distribution. Southern Palaearctic (from Iran, Turkey to Japan), Oriental region, Australia, Pacific (excl. Hawaiian Is).

KEY FOR THIRD INSTAR LARVAE AND PUPARIA

1 Angles between adjacent orificia about 90°, dorsal spur present (Figs 6A, B) (sg. *Semiscaeva*). 2
– Orificia II and III almost parallel, dorsal spur absent (Figs 6C, D). 4
2 Width of PRP about 0.5 mm or more; median groove deeper than half the length of PRP (Figs 8B, F). 3
– Width of PRP about 0.4 mm or less; median groove slightly less deep than half the length of PRP (Fig. 8D). . . . . *Scaeva (Semiscaeva) mecogramma*
3 Posterior folds coated with microtrichia with a wide base that become suddenly fine (Fig. 7A); some microtrichia of integumental vestiture pigmented apically; puparium usually with distinct dark dotted segmental pattern. . . . . *Scaeva (Semiscaeva) selenitica*
– Posterior folds coated with microtrichia with a wide base that become progressively fine to the apex (Fig. 7E); body coated with microtrichia of cuticle colour or almost so; puparium without dark dotted segmental pattern. . . . . *Scaeva (Semiscaeva) dignota*
4 Integumental vestiture distinct, microtrichia about 0.2–0.35 mm long on dorsum; microtrichia on posterior folds with thin apex (Figs 9A, C); orificia located on high oval carinae, slightly less developed in orificium III (Figs 10A, B, C) . . 5

TABLE 3. Sequence varibility in the variable regions of the ca 450 nt ITS2 (arbitrary alignment) that were obtained for all of the sequenced *S. dignota* specimens (genotype 1) and the *S. selenitica* specimens (genotype 2).

Genotype	Sequence varibility in the variable region of the ca 450 nt ITS2
S. dignota	....AGAGGATTATAGTATATAAAATTAAATCAAAGATATTAATATATAAAAATAAAAATATGTTTAAA--GAAGAAAAACCTAAGAAAAAAAAATATACTT....
S. selenitica	....AGAGGATTATAGTATATAAAATTAAA------------------TTAAAAATATAATTATGTTTAAAAAGTAAAACATAAATTAAAAAAAAAAATATACTT....

– Integumental vestiture reduced, microtrichia on dorsum about 0.02 mm long or shorter; microtrichia on posterior folds relatively broad near apex (Figs 9E, 11A); orificia located on very high oval carinae except orificium III located on distinctly less developed carina (10D, 11D, F). 6

5 Fold close to anterior part of PRP forming conical fleshy projection in median point (Fig. 1C), when dried, usually also apparent on puparium as a tubercle overlapping with PRP (Fig. 1D); ecdysial scars displaced towards the median groove and anteriorly (Fig. 10C). . . . . *Scaeva (Scaeva) albomaculata*

– Fold close to anterior part of PRP regularly rounded lateromedially without conical fleshy projection; ecdysial scars slightly anterior to centre of each spiracular plate (Figs 10A, B). . . . . *Scaeva (Scaeva) pyrastri*

6 Orificium III inserted only about 1/3 the length of orificium II posteriorly to orificium II; carina III distinct and carina I about as developed as carina II (Fig. 10D); fleshy projection under segmental spines less developed, not persist on puparium, so that segmental spines are sessile on puparium. . . . . *Scaeva (Scaeva) latimaculata*

– Orificium III inserted about half or more the length of orificium II posteriorly to orificium II; carina III almost flat and carina I enlarged, distinctly overlapping periphery of PRP (Figs 11D, F); fleshy projection under segmental spines more prominent, dried persist as microtrichose portion under segmental spines on puparium, especially on posterior part of dorsum (g. *Simosyrphus*). 7

7 Width of PRP about 0.3 mm or less; the most developed segmental spines about 0.1–0.14 mm long, in puparium elongated by microtrichose rests of dried fleshy projections nearly to 0.18 mm, especially on posterior part of dorsum. . . . . *Simosyrphus grandicornis*

– PRP wider than 0.35 mm; segmental spines longer, fully developed about 0.13–0.2 mm long, in puparium elongated by microtrichose rests of dried fleshy projections to about 0.2–0.3 mm, especially on posterior part of dorsum. 8

8 Width of PRP about 0.38–0.43 mm; fully developed segmental spines about 0.16–0.2 mm long, in puparium elongated by microtrichose rests of dried fleshy projection to about 0.3 mm, especially on posterior part of dorsum. . . . . *Simosyrphus aegyptius* comb. n.

– Width of PRP about 0.43–0.53 mm or longer; fully developed segmental spines about 0.13–0.18 mm long, in puparium elongated by microtrichose rests of dried fleshy projection nearly to 0.24 mm, especially on posterior part of dorsum. . . . . *Simosyrphus scutellaris* comb. n.

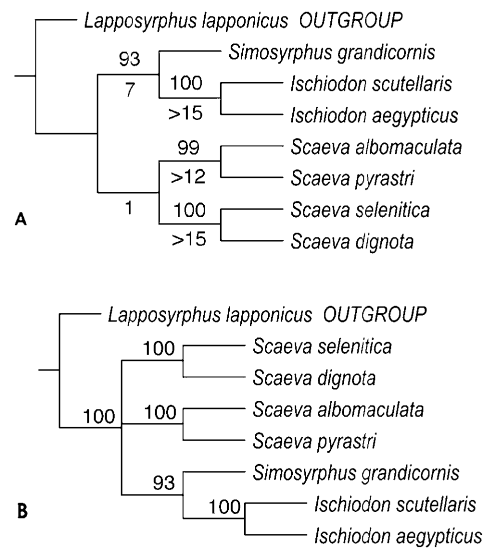

Fig. 12. A – Most parsimonious tree obtained using Nona for 1128 bp of the *cox1* gene, length = 224 steps, CI = 0.83, RI = 0.74. Bootstrap support values and Bremer support (branch support) values are reported above and below nodes, respectively. B – Parsimony jackknifing tree (1000 replicates).

MOLECULAR STUDIES

The parsimony analysis of 1128 nucleotides of the *cox1* gene of seven taxa belonging to *Scaeva* and *Simosyrphus,* using *Eupeodes (Lapposyrphus) lapponicus* as outgroup, produced one most parsimonious tree (Fig. 12A) of 224 steps (CI = 0.83; RI = 0.74). All proposed subgeneric and generic taxa based on morphological studies receive high bootstrap support (1000 replicates). We did not recover a closer relationship of sg. *Scaeva* with *Simosyrphus* than with sg. *Semiscaeva*, even if this node is suggested from the immature morphology (see Discussion). Resampling using jackknifing spawn from Winclada is shown in Fig. 12B.

Cox1 sequences of *Scaeva selenitica* and *S. dignota* were identical except for one nucleotide change in one *S. dignota* specimen. The six specimens of *S. dignota* presented identical ITS2 sequences (genotype 1, Table 3) and the five specimens of *S. selenitica* were also monomorphic for ITS2 (genotype 2). These two genotypes are distinct.

DISCUSSION

Taxonomy of *Scaeva*

According to our results, the Palaearctic *Scaeva* species can be split into two groups based on the analysis of immature stages. One group (*S. dignota, S. selenitica, S. mecogramma*) has a distinct angle of about 90° between orificia II and III, as is typical for other related genera of Syrphini. A second group (*S. pyrastri*, *S. albomaculata*, *S. latimaculata*) has the orificia II and III (on spiracular plate) parallel, with insertion of orificium III beneath the level of insertion of orificium II (probably apomorphic situation). These two groups that should be classified as subgenera were designated as natural groups within *Scaeva* by Dušek & Láska (1985) (*S. selenitica*-group vs *S. pyrastri*-group). Independently, Kuznetzov (1985) divided the Palaearctic *Scaeva* species in three subgenera based exclusively on adult morphology (*Semiscaeva*

Kuznetzov, 1985: 412, *Mecoscaeva* Kuznetzov, 1985: 418 and *Scaeva* s. str.). However, his arrangement of the species does not agree with the results of the present paper. The main differences are that following this author the species *S. mecogramma* (type species of subgen. *Mecoscaeva*), *S. dignota* (junior syn. of which is the type species of his subgen. *Semiscaeva*) and *S. selenitica* (from his subgen. *Scaeva*) are closely related on the basis of pre-imaginal and molecular data. According to our results they form a natural group that is identical to *S. selenitica*-group (sensu Dušek & Láska, 1985). The name *Semiscaeva* Kuznetzov, 1985 should be the valid name for the *S. selenitica*-group (sensu Dušek & Láska, 1985) as a subgenus of the genus *Scaeva*. The subgenus *Scaeva* s. str. can only be referred to the *S. pyrastri*-group (sensu Dušek & Láska, 1985) and as the first revisers we determine subgen. *Mecoscaeva* Kuznetzov, 1985 syn. n. as a junior synonym of subgen. *Semiscaeva* Kuznetzov, 1985.

Status of *Scaeva dignota* and *S. selenitica*

Scaeva dignota was recognized (from variability of *S. selenitica*) as a valid species by Dušek & Láska (1985). These authors observed that the anterior angle of approximation of eyes in males of *S. dignota* is narrow (90°–106°), face is narrower and ocular hairs are shorter in comparison with *S. selenitica*. The pattern of yellow spots on tergites 3 and 4 differs a little between the species. However, except for size differences of microtrichia of the posterior fold, we have been unable to found informative characters to distinguish larvae or pupae of these species. Moreover, these species present dichroism of larvae (green vs brown colour). We have observed this peculiar phenomenon only in these two species of the genus *Scaeva*. Male terminalia in both taxa are very similar. *S. dignota* is mainly a Mediterranean species and *S. selenitica* is a sub-boreal species (Dušek & Láska, 1985). The molecular analysis also indicated a very close relationship between these species, as both taxa presented identical *cox1* sequences in all the studied material (Czech, Spanish, Finnish and Greek specimens). This clearly supports that a separation of these two closely related species into different subgenera as done by Kuznetzov (1985) is unfounded. However, the nuclear ITS2 region sequenced for several *S. dignota* and *S. selenitica* from central Europe presented two different genotypes (Table 3). The utility of the mitochondrial *cox1* gene is limited when addressing questions about species delimitation between very closely related species, but the ITS2 proved to be informative even for these cases. The identical mitochondrial *cox1* sequences and divergent nuclear ITS2 could demonstrate a case of mitochondrial introgression between *S. selenitica* and *S. dignota*. The geographical distributions of both taxa overlap in the Central European Alps and warmer parts of Palaearctic (particularly Mediterranean).

Taxonomy of *Simosyrphus*

Vockeroth (1969) stated the close relation of *Ischiodon scutellaris*, *I. aegyptius* and *Simosyrphus grandicornis*. He mentioned several adult synapomorphies for the three species: similar habitus, colour pattern, a similar shape of head and a reduced antennal pedicel but elongated basoflagellomere. According to our new data, larval and pupal morphology also support the close relationship of these genera. The comparison of puparia of *Ischiodon* species with the puparium of *Simosyrphus grandicornis* reveals that the posterior respiratory process, as well as the whole puparium, are almost identical. The syrphid male terminalia are generally good indicators of relationships, but not in all cases. For example, *Eupeodes volucris* Osten Sacken, 1877, with enlarged and specialised genitalia, is now classified with the species from the previous genus *Metasyrphus* Matsumura, 1917 in a single genus (Vockeroth, 1986). Similarly, as in the case of *E. volucris*, we prefer uniting all known species of *Ischiodon* with *Simosyrphus grandicornis* considering the identical larval characters, even if *S. grandicornis* differs in the complicated and enlarged male terminalia. According to the results of this study we propose the generic name *Ischiodon* Sack, 1913 syn. n. as a junior synonym of the genus *Simosyrphus* Bigot, 1882.

CONCLUSIONS

The close relationship between *Simosyrphus*/*Ischiodon, Scaeva* and *Eupeodes* was established by Dušek & Láska (1985: p. 211) based on the special pattern of wing membrane and distinct morphology of larval PRP. Rotheray & Gilbert (1999) also showed the relationship of *Ischiodon* + *Eupeodes* + *Scaeva.* The character possessed by these three taxa is the presence of setae accompanying ventral sensillae of metathorax in larvae. We have found support for this feature with the additional taxa. However, there is a paradox: the PRP of *Scaeva* s. str. is more similar to that of *Simosyrphus* s. l. than to PRP of *Semiscaeva*. The general similarity in structure of PRP looks like a clear synapomorphy. This fact is supported also by the morphology of *Scaeva (Scaeva) latimaculata,* with similar thoracic coloration in adults and similar reduced integumental vestiture of larvae compared with *Simosyrphus* species. However, adult morphology of Palaearctic *Scaeva* s. l. species and *Simosyrphus* species is very different (including male terminalia). It could indicate that *Simosyrphus* had not long common evolution with most of the species of *Scaeva* s. str. Our molecular results do not resolve the relationship between Palaearctic *Scaeva* s. l. and *Simosyrphus*.

Finally, the placement of the Neotropical species referred to genus *Scaeva* is not resolved here. They form a separate monophyletic group (see Dušek & Láska, 1985: p. 226) that is probably sister to all Palaearctic *Scaeva* and *Simosyrphus* species according to the pattern of wing venation and other characters. They should be classified as a separated taxon (Mazánek & Láska, in prep.). The phylogenetic relationships of *Scaeva* and related genera will be reviewed in a further paper.

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