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

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**Key words.** Diptera, Syrphidae, *Scaeva*, *Semiscaeva*, *Mecoscaeva*, *Simosyrphus*, *Ischiodon*, taxonomy, immature morphology, chaetotaxy, new combination, new synonymy

**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 mecgrommata* (Bigot, 1860) and *Simosyrphus granicorius* (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 Palearctic *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. mecgrommata* (Bigot, 1860)] and *S. pyrastris*-group [i.e., *S. pyrastris* (Linnaeus, 1758), *S. albornamaculata* (Macquart, 1842), *S. latimaculata* (Brunetti, 1923)]. *Semiscaeva* Kuznetsov, 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. pyrastris*-group. *Mecoscaeva* Kuznetsov, 1985 syn. n. is transferred as a junior synonym of the subgenus *Semiscaeva* Kuznetsov, 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 granicorius* (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 & Bhatta, 1991; Xiong & Dong, 1991; Eukukole & Ajayi, 1995; Soleymean-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 (Láška, 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 & Láška (1985) and Kuznetsov (1985). However, these two revisions are quite different in species conceptions and in subgeneric classification. Recent authors usually follow the concept of Dušek & Láška (e.g. Speight, 2003), but up to now no nomenclatorical acts have been published to clarify this situation. The defence of Dušek & Láška’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 Palearctic (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 & Láška (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 & Láška (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 Palaeartic 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 (Stáhls & 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. Stáhls, 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. Alvarez & 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 University of 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 by hand. 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 & Láška (1964). The term orificium (Vimmer, 1925) was used instead of spiracular slits, and the term pterostigmata 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 described 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
selenitica and ITS2 genes of several specimens of the closely related species of the genus Scaeva, subgenus Semiacaeva Cox1 ITS2

<table>
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<th>Specimen</th>
<th>Genus and Subgenus</th>
<th>Location</th>
<th>Dates</th>
<th>Authors</th>
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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. pyrastrigrou...
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 Catahoma odessana Paramonov, 1924 (orig. des.) = S. dignota (Rondani, 1857).

**Subgenus Scaeva s. str.**
[S. pyrastri group sensu Dušek & Láska (1985)]

**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**

**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-
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 4th reduced, giving the integument a clear shining appearance (Fig. 2C). Anterior fold of prothorax with

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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 7th, ventral view.
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 7Mt and 9Mt shorter than others (Figs 3A, 5A, 4). One extra pair of sensory-organs near sensillae 7Ms and 7Mt (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 1A1 and 2 A1 located on the same fold. Second to seventh abdominal segments with the pair of segmental spines 1A2–7 on second fold and pair of segmental spines 2A2–7 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 1A7 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).
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 Kuznetsov, 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.
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 groove 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)


**Diagnostic characters.** The larva can present two patterns of colouration, green with a white median stripe (as in *S. pyrastrii*) 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).


**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: 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).


**Distribution.** Palaearctic, subboreal (see also discussion).
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).


**Distribution.** South Europe.
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.

*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*.
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).


Distribution. Sub-Mediterranean (see also discussion).
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 fuscate 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. Spiral 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)


*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 fuscate 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. Ecdyssal 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.
Scaeva albomaculata (Maqueurt, 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).


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. pyrastris, from which it differs by less developed integumental vestiture, microtrichia reduced to short, almost triangular spicles not longer than 0.02 mm, spicles 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).


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), Soleymen-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 middorsal 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♂, 8♂ and 9♂ (that was confirmed by our study of puparia); the locomotory prominences on 6♂ and 7♂ 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
intraspécific 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 intraspécific 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)

Soleymen-Nezhadiyan (1997) and Soleymen-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. Soleymen-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 dorsal of puparium as microtrichose portion (maximum length 0.05 mm). Microtrichia of cuticle colour or slightly 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).


**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 lepidopteran larvae were cited as preys by Randrianandrainiana-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).


**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). Ninomuya (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**

<table>
<thead>
<tr>
<th>1</th>
<th>Angles between adjacent orificia about 90°, dorsal spur present (Figs 6A, B)</th>
<th>2</th>
</tr>
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<tbody>
<tr>
<td>2</td>
<td>Orificia II and III almost parallel, dorsal spur absent (Figs 6C, D)</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>Width of PRP about 0.5 mm or more; median groove deeper than half the length of PRP (Figs 8D, F)</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>Width of PRP about 0.4 mm or less; median groove slightly less deep than half the length of PRP (Fig. 8D)</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>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</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>Pupa (Semiscaeva) selenitica</td>
<td>7</td>
</tr>
<tr>
<td>7</td>
<td>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</td>
<td>8</td>
</tr>
<tr>
<td>8</td>
<td>Pupa (Semiscaeva) megogramma</td>
<td>8</td>
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<tr>
<td>9</td>
<td>Pupa (Semiscaeva) dignota</td>
<td>9</td>
</tr>
<tr>
<td>10</td>
<td>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)</td>
<td>5</td>
</tr>
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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. pyrastris, 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. pyrastris-group). Independently, Kuznetzov (1985) divided the Palaearctic Scaeva species in three subgenera based exclusively on adult morphology (Semiscaeva...
He mentioned several adult synapomorphies for the three subgenus of the genus *S. selenitica* (sensu Dušek & Láska, 1985) as a *caeva* group (sensu Dušek & Láska, 1985). The name species of his subgen. *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. pyrastril*-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 find 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 syphid 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.

**ACKNOWLEDGEMENTS.** Special thanks to D. Hales (Australia) for rearing specially for us the puparia of *Simosyrphus grandicornis*, to H. Schmutterer (Giessen, Germany), A. Kumar (Ludhiana, India), B.K. Agarwala (Agartala, India) and E. Erkin.
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(IZmir, Turkey) who generously donated puparia in their care, to M. Hanáková and M. Štibnarová (Olomouc, Czech Republic) for their help with laboratory breedings and to E. Soleymaniehzadiyan (Ahwaz, Iran) for valuable information about larvae of S. grandicornis. We are greatly indebted to T. Petanidou (Greece) for the facilities to study material from Lesbos Island. Financial support was provided by the Spanish Ministry of Environment (040/2002) (C. P.-B., M.-G.), University of Alicante, Spain (GRE04-25) (C. P.-B., S.R) and from Finnish Ministry of Environment (G.S.).


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