

The first instar larva of *Apodacra pulchra* (Diptera: Sarcophagidae, Miltogramminae)

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The morphology of the first instar larva of the miltogrammine flesh fly *Apodacra pulchra* Egger, 1861 is described using SEM and light microscopy. The larva is shown to possess a strongly modified pseudocephalon with comb-like lateral processes, a large ventral organ, and a transversely enlarged, slit-like (or \perp -shaped) functional mouth opening. The thoracic cuticle is forming longitudinal ridges, and the abdominal segments have a single long lateral sensory sensilla on each side. Morphology is discussed in context of the remaining Oestroidea in general and of the subfamily Miltogramminae in particular.

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Introduction

Very little data are available on the morphology of the pre-imaginal stages of the flesh fly subfamily Miltogramminae. The main source of information on this topic is still that of Thompson (1921), who described the first (in some cases also the third) instar larva of ten European and two Nearctic species of Miltogramminae, representing the genera *Amobia* Robineau-Desvoidy, *Metopia* Meigen, *Miltogramma* Meigen, *Pterella* Robineau-Desvoidy, *Senotainia* Macquart, and *Sphenometopa* Townsend. Additional information on larval morphology of Miltogramminae is scanty and scattered in various papers, and it is mainly restricted to the shape of the cephalopharyngeal skeleton as reviewed by Ferrar (1987). Earlier studies mainly described material obtained by dissection of dried female specimens, as well as the puparium plus its associated third instar cephalopharyngeal skeleton.

The aim of the present work is to thoroughly describe the morphology of the first instar larva of *Apodacra pulchra* Egger, 1861 as a prerequisite for future phylogenetic studies. The genus *Apodacra* Macquart is represented by 43 described Old

World species occurring in the Afrotropical, Palaearctic, and Oriental regions (Pape 1996). Like most other Miltogramminae, all *Apodacra* species with known biology are kleptoparasites in nests of solitary wasps and bees (Séguy 1941, Myartzeva 1972, Verves 1979, Krombein & Pulawski 1986, Pape & Blasco-Zumeta 1996). In one case, larvae of *Apodacra dispar* Villeneuve, 1916 were found in a dead grasshopper (Holstein & Rudzinski 1994), possibly the abandoned prey of a sphecid wasp. Preimaginal stages of *Apodacra* spp. have remained unknown until now.

Apodacra pulchra is distributed from Central Europe to China (Neimenggu). The species prefers sandy areas, especially near river banks. Although suspected to be a kleptoparasite, nothing is known on the biology (Povolný & Verves 1997).

Material and methods

Two females (together with nine males) of *A. pulchra* were caught in a military training ground south of Toruń, northern Poland (UTM code: CD37). The area is characterized by many dunes, partly overgrown with psammophilous grasses and

shrub vegetation, and fragments of pine stands (*Pinus sylvestris* L.) spontaneously regenerating after frequent fires. Both females were caught in an area with numerous nests of the sphecoid wasps *Bembix rostrata* (Linnaeus), *Miscofus bicolor* Jurine, and *Bembecinus tridens* (Fabricius), and the pompilid wasp *Pompilus cinereus* Fabricius.

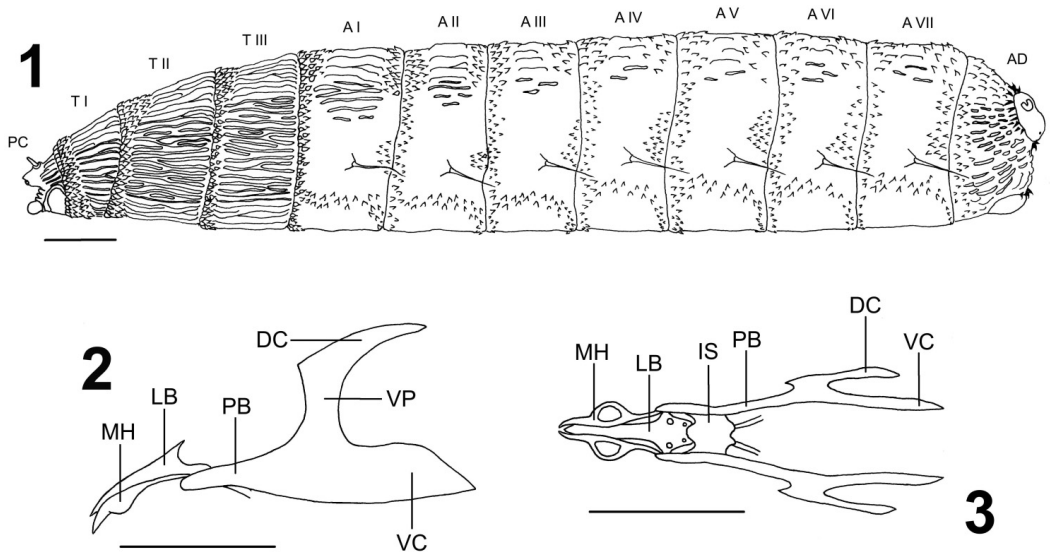
To obtain larvae, each freshly caught female was kept in a 150 ml glass jar with a finely perforated cover and with a layer of filter paper in the bottom. During the following three days both females spontaneously and repeatedly larviposited, and the first instar larvae were immediately collected. After the death of both females on day three after capture, additional larvae were extracted from their abdomen by carefully cutting the membrane between segments VI and VII and gently squeezing the abdomen. Both females were subsequently pinned and labelled (deposited in coll. Szpila). In total, 23 first instar larvae were obtained, 13 of which were fully developed. Larvae were killed by soaking in hot water to avoid deformation and stored in 70% alcohol.

Larvae were slide-mounted in Euparal and Hoyer's medium. Illustrations were produced from photographs made with the use of a digital Nikon

DMX 1200 camera mounted on a Zeiss Axioplan 2 microscope. SEM pictures were taken with the use of a Jeol Scanning Microscope JSM-6300, for which larvae were dehydrated through 80, 90, and 99.5% ethanol, critical point dried in CO₂, and coated with gold.

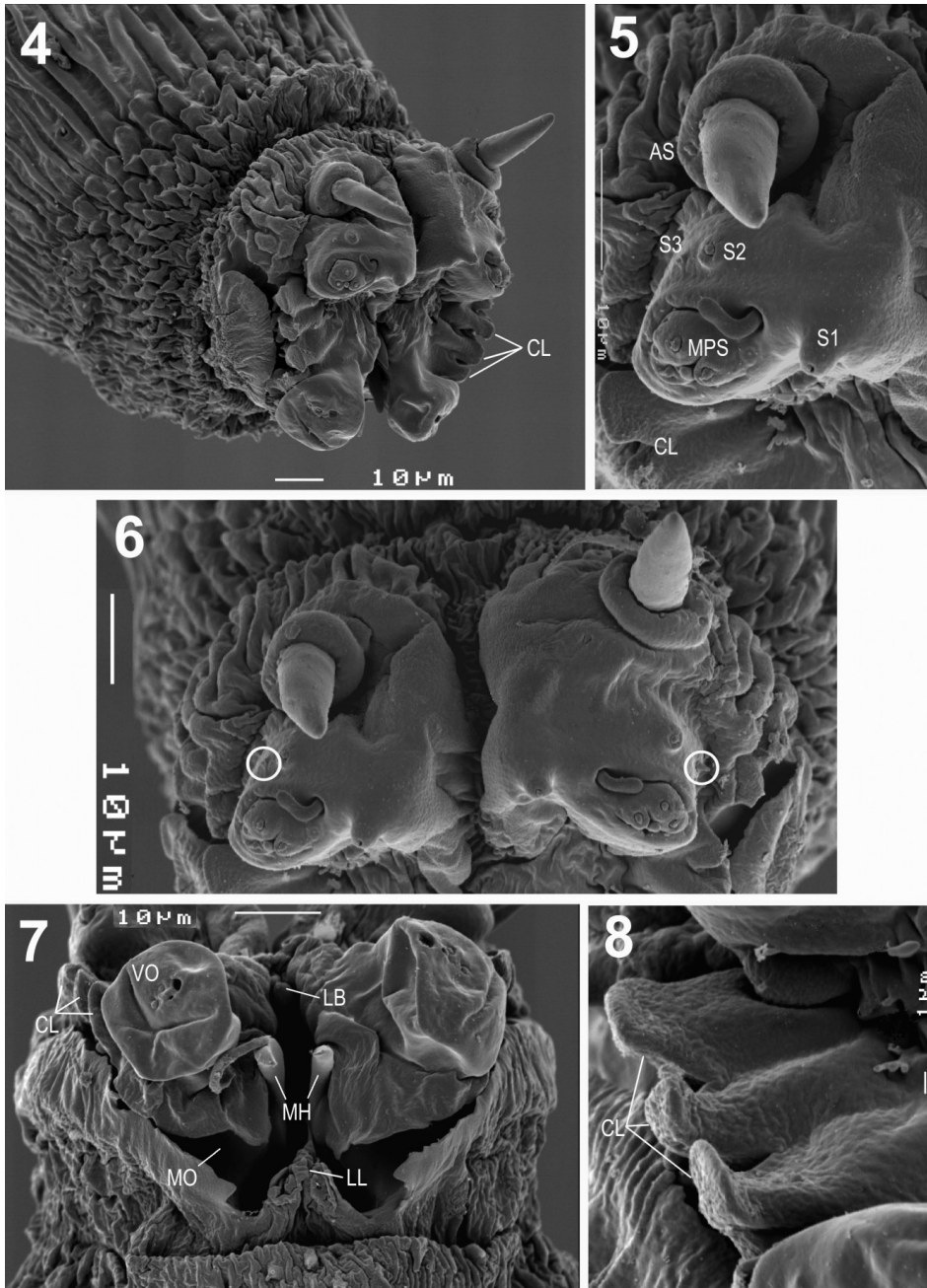
Terminology

Cyclorrhaphan Diptera larvae are strongly modified, and structures on the reduced head are particularly difficult to homologize with adult structures. We are here using the terminology of Courtney *et al.* (2000), using "pseudocephalon" for the part of the body anterior to the first thoracic segment ("cephalic region" of Meier 1996). The robust cone- or peg-like structure set in a more or less well-developed cuticular ring or socket antero-dorsally on the pseudocephalon is referred to as the antenna. A raised area below the antenna, containing a large cluster of sensilla, is referred to as the maxillary palp ("maxillary papilla" of Schmidt 1993, "maxillary sensory complex" of Colwell & O'Connor 2000), here used in the broad sense including the pair of apparently non-maxillary sensilla, one of which is considered as origi-



Figs 1-3. First instar larva of *Apodactra pulchra* Egger, 1861. – 1. Whole body, lateral view. – 2. Cephalopharyngeal skeleton, lateral view. – 3. Cephalopharyngeal skeleton, ventral view. Scales = 0.1 mm.

Abbreviations: AI-AVII = abdominal segments, AD = anal division, DC = dorsal cornua, IS = intermediate sclerite, LB = labrum, MH = mouthhook, PB = parastomal bar, PC = pseudocephalon, TI-TIII = thoracic segments, VC = ventral cornua, VP = vertical plate.



Figs 4-9. First instar larva of *Apodacra pulchra* Egger, 1861. – 4. Anterior end, antero-lateral view. – 5. Lobe of pseudocephalon, anterior view. – 6. Pseudocephalon, anterior view, showing dorso-lateral separated maxillary sensillum (S3, marked with ring). – 7. Pseudocephalon, ventral view. – 8. Pseudocephalon, comb-like structure. Abbreviations: AS = antennal socket sensillum, CL = comb-like structure, LB = labrum, LL = labial lobe, LP = lateral papillae, MH = mouthhooks, MO = functional mouth opening, MPS = clustered maxillary palp sensilla, S1 = middle separated maxillary sensillum, S2 = dorsal separated maxillary sensillum, S3 = dorso-lateral separated maxillary sensillum, VO = ventral organ.

nating from the antennal segment, while the other may be of either antennal or mandibular origin (see references in Courtney *et al.* 2000). The latter two sensilla were referred to with the topographical term "dorso-lateral sensilla of maxillary papilla" by Schmidt (1993), but as their position on the maxillary palp may differ considerably from a dorso-lateral position, as will be discussed further below, we will use the ontogenetically neutral term "separated sensilla of maxillary papilla", awaiting further studies on homology. Below the maxillary palp and anterior to the functional mouth opening is the ventral organ ("maxillary organ" of Schmidt 1993), the origin and homology of which likewise is in dispute (Jürgens *et al.* 1986, Hartenstein 1988). The three thoracic segments are denoted as TI–TIII and the abdominal segments as AI–AVII plus the anal division (the last 'segment' is ontogenetically a composite of several morphological segments).

Results

The first instar larva of *A. pulchra* has a distinct pseudocephalon, which is divided sagittally to form two lobes with a complicated structure (Fig. 4). Each of the two pseudocephalic lobes has a long antennal peg situated in a distinct socket on the dorsal surface (Figs 5, 6, 13). The antennal socket has a small ventro-lateral sensillum (Fig. 5). The cuticle behind the antennae is strongly wrinkled by short, longitudinal folds (Fig. 4). The maxillary palp is a low, dome-like structure situated on the anterior surface of the protruding upper part of the pseudocephalic lobe [i.e., dorsal to the labrum] (Fig. 5). In the central part of the maxillary palp is a cluster of five distinct peg sensilla (MPS), three set in swollen sockets and two non-socketed, plus at least one additional indistinct sensillum almost level with the surrounding cuticle. The peg of both non-socketed sensilla have a swollen or rounded tip, and the uppermost of these two sensilla is elongated, curved dorso-laterally, and set at a short distance from the main cluster of sensilla. Three socketed peg sensilla (S1–S3) are found along the periphery of the maxillary palp ("separated sensilla", Figs 5, 6). One sensillum (S1) is mediad of the MPS cluster and set on a large, cone-like socket close to the cleft between the antenno-maxillary lobes; another is dorsal to the cluster (S2), and the third is dorso-lateral to the cluster and has a pointed peg in a very reduced

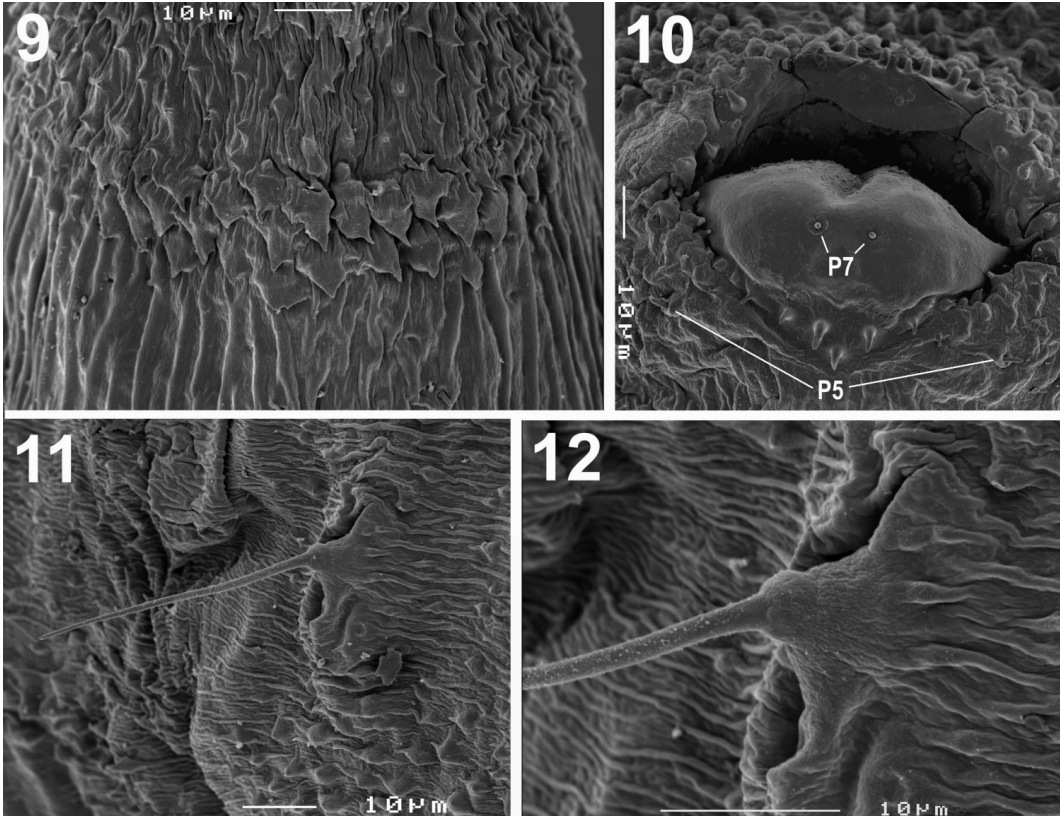
socket (S3). A marked difference in size of the peg of the left and right dorso-lateral separated sensilla (S3) was observed (Fig. 6, circles) but cannot be explained without further observations.

Below the protruding upper part of the pseudocephalon are three slate-like processes arranged as laterally-directed, comb-like structures (Figs 4, 8, CL). Situated close to the ventral (lower) part of the comb, the ventral organ (VO) is shaped like a swollen, bladder-like structure with a cluster of sensilla on the flattened, anteriormost surface, including two pit sensilla (one very prominent), and two peg sensilla (Figs 4, 7). The functional mouth opening (MO) consists of the usual longitudinal furrow between the ventral organs and in which labrum and mouthhooks are lodged, plus a very broad U-formed slit starting from the lateral surface of the pseudocephalic lobe at the level of the maxillary palp, running ventral just posterior to the comb-like row of slate-like structures and intersecting with the longitudinal slit behind and below the ventral organs (Fig. 7). The labrum projects between the ventral organs as a simple tooth-like process (Figs 4, 7, LB). Slender pointed tips of the mouthhooks are visible below. The triangular labial lobe forms the postero-median part of the mouth opening. It is equipped with a pair of distal sensilla (Fig. 7, LL).

The cephalopharyngeal skeleton consists of an unpaired labrum, paired mouthhooks, unpaired intermediate sclerite, paired parastomal bars, paired lateral plates, each with ventral and dorsal cornua (Figs 2, 3, 14). The labrum is strongly sclerotised and pointed. The base of labrum has two pairs of openings (Fig. 3). The middle part of the mouthhook is widened in the horizontal plane by a flat, lateral extension with a large opening (or concavity?) in the central part (Fig. 3). The intermediate sclerite is located between the parastomal bars. No dorsal bridge is present.

Segments TI–TIII are equipped with narrow anterior bands of spines (Fig. 1), and the remaining surface is arranged in numerous cuticular ridges parallel with the longitudinal axis of the body (Figs 1, 4, 9). Single lateral papillae occur on TI–TIII (Fig. 4, LP).

Segments AI–AVII are equipped with anterior bands of spines similar to those on the thoracic segments. Segments AI–AVII posteriorly with dorsal and lateral separated clusters of spines, which on AVI–AVII fuse to form an irregular and incomplete posterior spine band (Fig. 1). Cuticular lon-

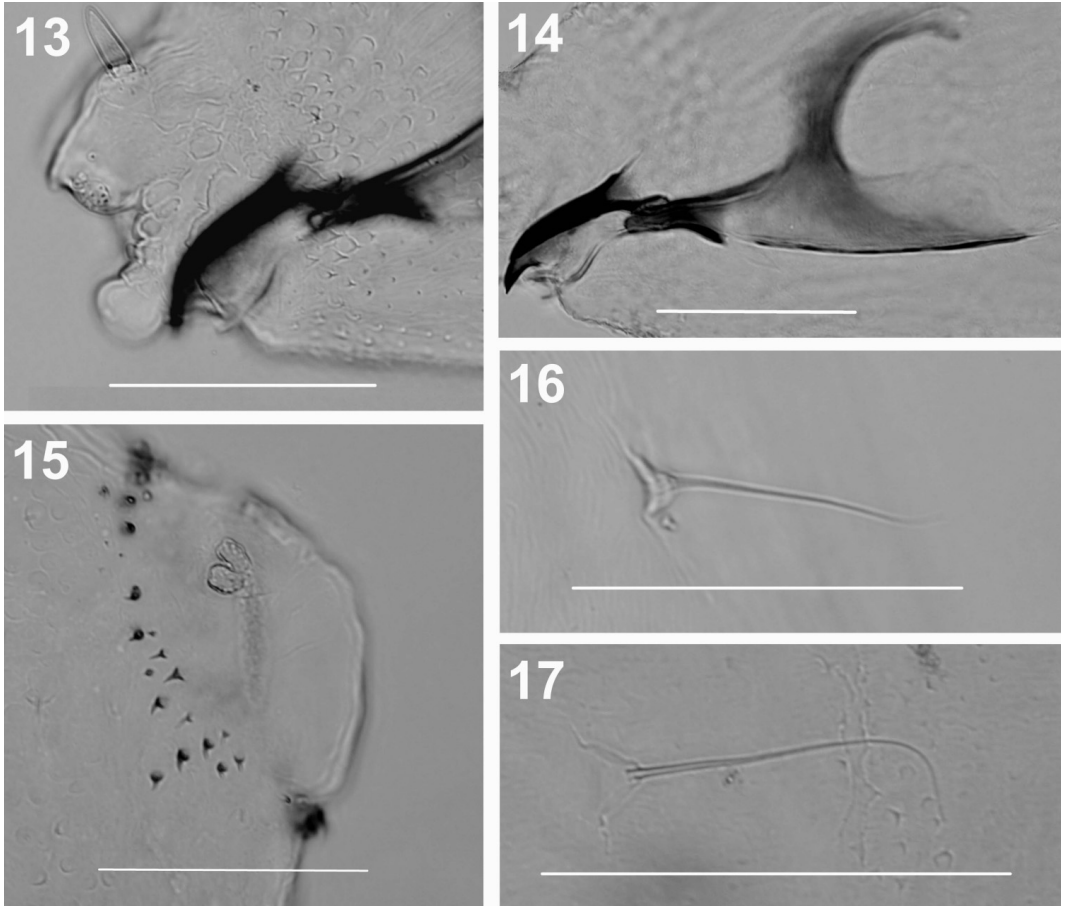


Figs 9-12. First instar larva of *Apodacra pulchra* Egger, 1861. – 9. TII-TIII, ventral view. – 10. Spiracular cavity, posterior view. – 11. Bristle-like sensillum. – 12. Base of bristle-like sensillum. Abbreviations: P5 = subventral papillae, P7 = supraventral papillae.

gitudinal ridges are well developed only on the dorsal surface, except for the anal division, which has ridges also laterally (Fig. 1). The dorsal longitudinal ridges are gradually reduced in length and in numbers from AIII to AVII. The lateral surface of each of AI-AVII has a long, bristle-like sensillum originating from a spherical base (Figs 1, 11, 12, 16, 17). Ventral to the bristle-like sensillum is a narrow horizontal band of spines running from the anterior spine band to the posterior margin, connecting along the ventral side with its counterpart (Fig. 1). The posterior spiracular field has the form of a convex, lens-shaped protuberance (Figs 1, 15). This protuberance may be pulled into the spiracular cavity (Fig. 10). Around the spiracular field and anal opening are several sharp spines (Fig. 15). Two pairs of peg-sensilla are present on the anal division (Fig. 10, P5, P7).

Discussion

A remarkable feature of the general habitus of the first instar larva is the strong cuticular longitudinal ridges, which are numerous on the upper part of the pseudocephalon, the entire surface of all thoracic segments, more sparsely arranged dorsally on abdominal segments AI-AVII, and dorsally and laterally on the anal division (Fig. 1). These ridges are unlikely to be artifacts (e.g., due to the killing by soaking in hot water and/or the critical point drying) as larvae of *Pollenia* showed no such cuticular ridging after an identical treatment (Szpila, 2003). Similar cuticular ridges have been illustrated for, or at least stated to occur in, the genera *Metopia*, *Miltogramma*, *Pterella*, and *Senotainia* by Thompson (1921), while they were noted to be absent in *Sphenometopa* (“La peau ne présente pas de côtes longitudinales”, Thompson



Figs 13-17. First instar larva of *Apodacra pulchra* Egger, 1861. – 13. Pseudocephalon, lateral view. – 14. Cephalopharyngeal skeleton, lateral view. – 15. Posterior body end, lateral view. – 16-17. Bristle-like sensillum. Scales: Fig. 15 = 0.05 mm, others = 0.01 mm.

1921:107). No other oestroid first instar larvae have a similar cuticular modification, which is evidence that this character state is autapomorphic for all or at least a large subset of the Miltogramminae.

The pseudocephalon is more complex and more elaborate than typically in the Oestroidea. The antenna is about 2-3 x as long as in other Miltogramminae (cf., Thompson 1921), other Sarcophagidae (e.g., *Sarcophaga aldrichi* Parker, see Schmidt 1993), and many Calliphoridae (e.g., *Pollenia* spp., see Szpila 2003). The maxillary palp is similar to that found in many other Cyclorrhapha in having a cluster of five peg-like sensilla, three set in a distinct socket plus two without sock-

ets (e.g., Courtney *et al.* 2000). However, the arrangement differs markedly by one of the non-socketed sensilla being distinctly elongated, slightly swollen apically, and slightly removed from the remaining sensilla. The maxillary palp has only been superficially documented by Thompson (1921:87, his fig. 90), who records the elongated sensillum in species of the genus *Miltogramma* but leaves no information on this structure for the remaining species in his study. Ongoing studies (Szpila & Pape in prep.) indicate that the elongated non-socketed sensillum is widespread in the Miltogramminae, suggesting that this feature may be autapomorphic at a basal level in the subfamily.

The proper recognition and homologization of the dorso-lateral (and possibly non-maxillary) sensilla is not straightforward as the arrangement in *Apodacra pulchra* deviates significantly from the widespread and possibly plesiomorphic condition in the Cyclorrhapha, in which two almost equal-sized sensilla are set in a dorso-lateral position.

The ventral organ is well developed and set as prominent swellings flanking the labrum and mouthhooks, contrasting with a much more modest development of this organ in other Oestroidea, e.g. Sarcophaginae (Schmidt 1992, Colwell & O'Connor 2000) and in the Calliphoridae (Leite & Guevara 1993; Sukontason *et al.* 2003a,b; Szpila 2003).

Long, lateral sensory structures on the abdominal segments have not previously been reported from first instar larvae of the Sarcophagidae but are found scattered in the Oestroidea, e.g., the Rhinophoridae (Pape & Arnaud 2001) and the peculiar rhiniine genus *Villeneuveiella* (Grünin 1957). However, these structures seem to be more fleshy and thicker and of more complex build than the ones reported in *Apodacra*.

The anal division has only two pairs of papillae, which possibly are homologous to the subventral (P5) and supraventral (P7) papillae in first instar larvae of the Calliphoridae (Erzinçlioğlu 1985, Szpila 2003).

Significant modifications of the first instar pseudocephalon have been documented for the flesh fly genera *Panava* Dodge and *Titanogrypa* Townsend of the subfamily Sarcophaginae. In these cases the surface of the pseudocephalon is sclerotised, which has been considered an adaptation for predation (Lopes 1943, 1978). While it may be premature to speculate on the adaptational value of the complex modifications of the pseudocephalon and the cuticular folds in *Apodacra*, it is tempting to suspect that the evolution of these features may be associated with the miltogrammine kleptoparasitic habit, possibly a combination of improved sensorial equipment for localizing the prey stored for the host progeny, and coping with a very dry, sandy environment. Other calliphorid and sarcophagid larvae with a somewhat comparable free-living stage of the newly hatched first instar larva, however, do not show comparable modifications. The first instar larva of European *Pollenia* Robineau-Desvoidy and of *Sarcophaga* Meigen (*sensu stricto*) are predators or parasitoids of earthworms. The first instar larvae of these taxa

will actively locate their prey or hosts in their burrows, yet their external morphology is not particularly modified (Szpila 2003, Szpila & Pape unpubl.). It is noteworthy, however, that low levels of soil moisture inhibits oviposition in *Pollenia pediculata* Macquart (Thomson & Davies 1973) and several other *Pollenia* spp. (Szpila, unpubl.). First instar larvae of Rhinophoridae are equipped with scale-like spines that may reduce water loss in their free-living stage (Bedding 1973, Pape & Arnaud 2001), but the first instar larva of the tumbu fly, *Cordylobia anthropophaga* (Blanchard & Bérenger-Féraud), which is known for its ability to wait for hosts in dry sand for up to two weeks, has its segments only partially covered with minute spines (Zumpt 1965).

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References

- Bedding, R.A. 1973. The immature stages of Rhinophorinae (Diptera: Calliphoridae) that parasitise British woodlice. - *Transactions of the royal Entomological Society of London* 125: 27-44.
- Colwell, D.D. & O'Connor, M. 2000. Scanning electron microscopy of sarcophagid (Diptera) larvae recovered from a case of human cutaneous myiasis. - *Journal of Medical Entomology* 37: 854-859.
- Courtney, G.W., Sinclair, B.J. & Meier, R. 2000. Morphology and terminology of Diptera larvae. Pp. 85-161 in: Papp, L. & Darvas, B. (eds), *Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance)*. Science Herald Press, Budapest.
- Erzinçlioğlu, Y.Z. 1985. Immature stages of British *Calliphora* and *Cynomya*, with re-evaluation of the taxonomic characters of larval Calliphoridae (Diptera). - *Journal of Natural History* 19: 69-96.
- Ferrar, P. 1987. A guide to the breeding habits and immature stages of Diptera Cyclorrhapha. *Entomograph* 8: 1-907. [2 vols.]
- Grünin, K.Ya. 1957. Neue Arten der Gattung *Villeneuveiella* Austen (*Rhynchoestrus* Ségué) aus UdSSR und Iran (Diptera, Calliphoridae). - *Entomologicheskoe obozrenie* 36: 538-546. [In Russian with German summary]
- Hartenstein, V. 1988. Development of *Drosophila* larval sensory organs: spatiotemporal pattern of sensory neurons, peripheral axonal pathways and sensilla differentiation. - *Development* 102: 869-886.

- Holstein, J. & Rudzinski, H.-G. 1994. A remarkable record of *Apodacra dispar* Villeneuve, 1916 (Diptera, Sarcophagidae, Miltogrammatinae) from southeast of Spain. - *Studia dipterologica* 1: 114-121.
- Jürgens, G., Lehman, R., Schardin, M. & Nüsslein-Volhard, C. 1986. Segmental organization of the head in the embryo of *Drosophila melanogaster*. - *Roux's Archives of Developmental Biology* 195: 359-377.
- Krombein, K.V. & Pulawski, W.J. 1986. Biosystematic studies of Ceylonese wasps, XVI: A revision of *Gastrosericus* Spinola (Hymenoptera: Sphecoidea: Larridae). - *Smithsonian Contributions to Zoology* 436: iii, 1-20.
- Leite, A.C.R. & Guevara J.D.E. 1993. Scanning electron microscopy of the larval instars of *Cochliomyia hominivorax*. - *Medical and Veterinary Entomology* 7: 263-270.
- Lopes, H.S. 1943. Contribuição ao conhecimento das larvas dos Sarcophagidae com especial referência ao esqueleto cefálico (Diptera). - *Memórias do Instituto Oswaldo Cruz* 38: 127-163. [In Portuguese with English summary.]
- Lopes, H.S. 1978. The systematic position of the genus *Panava* Dodge with descriptions of two new species (Diptera, Sarcophagidae). - *Revista brasileira de Biologia* 38: 801-805.
- Meier, R. 1996. Larval morphology of the Sepsidae (Diptera: Sciomyzoidea) with a cladistic analysis using adult and larval characters. - *Bulletin of the American Museum of Natural History* 228: 1-147.
- Myartzeva, S.N. 1972. [The parasites and predators of the sphecoid wasps in Turkmenia.] Pp. 101-115 in: Tokgaev, T. & Myartzeva, S.N. (eds), [The Insects of southern Turkmenia, Ashkhabad.] Akademia Nauk Turkmenskoi SSR, Ashkhabad. [In Russian.]
- Pape, T. 1996. Catalogue of the Sarcophagidae of the world (Insecta: Diptera). - *Memoirs of Entomology, International* 8: 1-558.
- Pape, T. & Arnaud, P.H., Jr. 2001. *Bezzimyia* - a genus of New World Rhinophoridae (Insecta, Diptera). - *Zoologica Scripta* 30: 257-297.
- Pape, T. & Blasco-Zumeta, J. 1997. *Apodacra cyprica* Rondani (Diptera: Sarcophagidae) bred from *Euodynerus variegatus* (Fabricius) (Hymenoptera: Eumenidae) in Spain. - *Zapateri Revista aragonesa de Entomologia* 6: 93-95.
- Povolný, D. & Verves, Yu.G. 1997. The flesh-flies of Central Europe (Insecta, Diptera, Sarcophagidae). - *Spixiana Supplement* 24: 1-260.
- Schmidt, J.M. 1993. A comparison of the sensory morphology of the cephalic region of first- and third-instar *Arachnidomyia aldrichi* (Parker) (Diptera: Sarcophagidae). - *Canadian Entomologist* 125: 101-111.
- Séguy, É. 1949. Diptères du Sud-Marocain (Vallée du Draa) recueillis par M.L. Berland en 1947. *Revue Française d'Entomologie* 16: 152-161.
- Sukontason, K.L., Sukontason, K., Lertthamnongtam, S., Kuntalae, B., Thijuk, N., Vogtsberger, R.C., Olson, J.K. 2003a. Surface ultrastructure of *Chrysomya rufifacies* (Macquart) larvae (Diptera: Calliphoridae). - *Journal of Medical Entomology* 40: 259-267.
- Sukontason, K.L., Sukontason, K., Piangjai, S., Boonchu, N., Chaiwong, T., Vogtsberger, R.C., Kuntalae, B., Thijuk, N., Olson, J.K. 2003b. Larval morphology of *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae) using scanning electron microscopy. - *Journal of Vector Ecology* 28: 47-52.
- Szpila, K. 2003. First instar larvae of nine West-Palaearctic species of *Pollenia* Robineau-Desvoidy, 1830 (Diptera, Calliphoridae). - *Entomologica Fennica* 14: 193-210.
- Thompson, W.R. 1921. Recherches sur les diptères parasites. I - Les larves des Sarcophagidae. - *Bulletin Biologique de la France et Belge* 54: 313-463, pls 6-18. [Also published with separate pagination 1-151.]
- Thomson, A.J., Davies D.M. 1973b. The biology of *Pollenia rudis*, the cluster fly (Diptera: Calliphoridae). II. Larval feeding behaviour and host specificity. - *Canadian Entomologist* 105: 985-990.
- Verves, Yu. G. 1979. Review of the subfamily Miltogrammatinae (Diptera, Sarcophagidae) of Sri Lanka. - *Entomologicheskoe obozrenie* 58: 883-897. [In Russian, English translation in *Entomological Review, Washington* 58: 159-173.]
- Verves, Yu. G. 1989. The phylogenetic systematics of the miltogrammatine flies (Diptera, Sarcophagidae) of the world. - *Japan Journal of Medical Science and Biology* 42: 111-126.
- Zumpt, F. 1965. *Myasis in man and animals in the Old World*. Butterworths, London, 267 pp.

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