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OMALUS SCULPTICOLLIS AS THE MAIN ENEMY OF PSENULUS FUSCIPENNIS (HYMENOPTERA: CHRYSIDIDAE, CRABRONIDAE) IN THE CRIMEA, UKRAINE

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***Omalus sculpticollis* as the Main Enemy of *Psenulus fuscipennis* (Hymenoptera, Chrysididae, Crabronidae) in the Crimea, Ukraine.** Martynova K. V., Fateryga A. V. — The trap-nest technique was tested in the Karadag Nature Reserve (Crimea, Ukraine). In the result the enemies of *Psenulus fuscipennis* (Dahlbom, 1843), which caused damage to its progeny, were revealed: *Omalus sculpticollis* Abeille, 1878, *Melittobia acasta* Walker, 1839, *Perithous septemcinctorius* (Thunberg, 1822), and *Trichodes apiarius* Linnaeus, 1758. The structure of the parasite complex, voltinity of the species, comparative effectiveness of enemies are determined on the basis of observed data. The taxonomical position of *O. sculpticollis* is discussed, its sexual dimorphism is illustrated, the detailed description of the cocoon and some structural features of the last instar larva are given for the first time. Feeding habits of the larvae of *O. sculpticollis* are examined and the delicate aspects of interaction with the host are discussed. Short notes on terminology are given.

Key words: *Omalus sculpticollis*, *Psenulus fuscipennis*, host-parasitoid relationships, cocoon, larva, carnivoroid, Karadag Nature Reserve, Crimea, Ukraine.

***Omalus sculpticollis* как главный враг *Psenulus fuscipennis* (Hymenoptera, Chrysididae, Crabronidae) в Крыму, Украина.** Мартынова Е. В., Фатерыга А. В. — Установка гнезд-ловушек на территории Карадагского природного заповедника (АР Крым, Украина) позволила выявить следующих врагов, вредящих потомству осы *Psenulus fuscipennis* (Dahlbom, 1843): *Omalus sculpticollis* Abeille, 1878, *Melittobia acasta* Walker, 1839, *Perithous septemcinctorius* (Thunberg, 1822) и *Trichodes apiarius* Linnaeus, 1758. На основе полученных данных установлены: структура паразитарного комплекса, вольгинность видов, сравнительная эффективность различных насекомых как врагов. В отношении *O. sculpticollis* обсуждено таксономическое положение вида, проиллюстрирован половой диморфизм, впервые даны подробное описание кокона и некоторые черты строения личинки последнего возраста, проанализированы характер и способ питания личинок, обговорены тонкие аспекты взаимодействия с хозяином, приведены краткие замечания к терминологии.

Ключевые слова: *Omalus sculpticollis*, *Psenulus fuscipennis*, хозяино-паразитные отношения, кокон, личинка, карниворойд, Карадагский природный заповедник, Крым, Украина.

Introduction

The trap-nest technique is one of the most frequently used methods for determining the host-parasitoid relationships in Hymenoptera. As noted by Krombein (1967) “the method of attack by the adult parasitoid, the degree of host specificity, comparative effectiveness of the various species as parasites, mode of attack by the chrysidid larvae and specificity of their cocoons, degree of synchrony in development with that of the hosts and specificity of the cocoons are all of considerable interest”.

The method of trap-nests, which were used for determining the species composition of solitary wasps and bees in the Karadag Nature Reserve (the Crimean peninsula, Ukraine) (Ivanov et al., 2009), provided an opportunity to study also the case of *Psenulus fuscipennis* (Dahlbom, 1843) with special reference to its associates.

The genus *Psenulus* Kohl, 1897 includes about 160 species, of which 10 have been found in Europe (Tormos et al., 2005). Two species — *P. fuscipennis* and *P. pallipes* (Panzer, 1798) — have been registered in the Karadag Nature Reserve (Shorenko, 2005).

Psenulus fuscipennis is a widely distributed Palaearctic species (Nemkov, 2009), its areal is disjunctive as it has a spot in Siberia (Nemkov, 1998). All species of the genus *Psenulus* nest in cavities, such as hollow stems of plants (elderberry, sumac, ash, bamboo, etc.) and abandoned borings of xylophagous insects in wood (Bohart, Menke, 1976; Kazenas, 2000). *Psenulus fuscipennis* is also known to nest in hollow stems of *Phragmites australis* and *Heracleum*, and xylophages' mines (Bonelli, 1988). Subsequently, its nests appear to be the linear nonbranching ones (according to Radchenko, Pesenko, 1994). Grandi (1961) reported lachnine aphids in the genus *Cinara* Curtis, 1835 (Homoptera, Lachnidae) as the prey stored by the species; the number of aphids per cell can amount up to 40–60 individuals according to Bonelli, and 30–50 according to Grandi (Bonelli, 1988). The prey consists of both nymphs and adults in nearly all cases (Bohart, Menke, 1976). The following chrysidid wasps were reported as enemies of *P. fuscipennis* in South-Western Ukraine: *Omalus (Chrysellampus) truncatus* Dahlbom, 1831, *O. (s. str.) violaceus* (Scopoli, 1763) and *Chrysis (Trichrysis) cyanea* (Linnaeus, 1758) (Kilimnik, 1993).

Wasps belonging to the family Chrysididae lay eggs into the nests of other Hymenoptera (solitary wasps and bees), into the cocoons of sawflies and silk moths (Limacodidae), and into the eggs of walking stick insects (Phasmatidae). Chrysidid larvae feed on the progeny of the insects mentioned above, but they can also consume the prey stored in the nests such as spiders, true bugs, aphids, thrips (Kimsey, Bohart, 1991).

Omalus (Chrysellampus) sculpticollis Abeille, 1878 is the only chrysidid wasp, which invaded the nests of *P. fuscipennis* in the Crimea. It is a rather rare species, though it can be locally abundant (Rosa, 2005 a). The range of its distribution includes Southern Europe, Western Asia, and the South of the former USSR (Berland, Bernard, 1938; Linsenmaier, 1959 a, b; Móczár, 1967; Kimsey, Bohart, 1991). The attributed chorological pattern is South-European (Agnoli, Rosa, 2011).

Material and methods

The material for the present study was obtained by placing the trap-nests throughout the Karadag Nature Reserve (department of the National Academy of Sciences of Ukraine) in 2005, 2009, 2010, and 2011. Trap nests were fabricated from the hollow stems' sections of *Phragmites australis* and other plants (*Rubus*, *Rumex*, *Carduus*), which were grouped in Fabre's hives and sheaves (fig. 1). The sheaves contained different number of nest tubes (from 7 to 133) and the diameter of the latter varied from 3 to 12 mm (Ivanov et al., 2009). Every year the trap nests were placed in the reserve during the first warm days of spring. In autumn the trap nests were removed, opened and examined in the laboratory. The stems containing the nests of *P. fuscipennis* were left to overwinter in natural conditions. An in-depth inspection of these nests was carried out the following April. Nests and cells inside were numbered. The innermost cell was considered to be the first one, as it had been constructed earliest. The contents of each cell were identified and noted in a diary preserving the same order observed in the nest. When opened in April, we found prepupae or pupae enclosed in cocoons. We placed the contents of the cells into glass vials to mature. When the emergence of imagoes took place, it was possible to identify the occupants and their associates.



Fig. 1: a — the landscape of the Karadag Nature Reserve; b — the Fabre's hive (photo by S. P. Ivanov).

Рис. 1: a — ландшафт Карадагского природного заповедника; b — улей Фабра (фото С. П. Иванова).

Psenulus fuscipennis (Dahlbom, 1843)

In total 95 nests of *P. fuscipennis* were obtained. The diameter of stems with wasp nests varied from 5.0 to 7.7 mm; the number of cells per nest varied from 5 to 31 (mode — 18, average — 16.5). The total number of cells was 1503. Mortality was observed in 97 (6.5 %) cells: in 68 cases at the egg stage, in 29 cases as young larvae.

Other 621 (41.3 %) cells of *P. fuscipennis* were occupied or destroyed by different wasp enemies:

435 — by *Omalus sculpticollis* Abeille, 1878 (Hymenoptera, Chrysididae), though only 90 specimens of *O. sculpticollis* were found in the nests overall;

116 — by *Melittobia acasta* Walker, 1839 (Hymenoptera, Eulophidae);

38 — by *Trichodes apiarius* (Linnaeus, 1758) (Coleoptera, Cleridae);

32 — by *Perithous septemcinctorius* (Thunberg, 1822) (Hymenoptera, Ichneumonidae (fig. 2)).

The final results are that *O. sculpticollis* is the main regulator of *P. fuscipennis* abundance. As a consequence, only the 52.2 % of *P. fuscipennis* emerged from their nests. *Psenulus fuscipennis* were at a prepupal or pupal stage during the examination of the nests in the third decade of April. The emergence of imagoes took place about two months later, at the end of June. Consequently, we conclude that this species overwinters as prepupa enclosed in cocoon.

Previously *P. fuscipennis* was reported as monovoltine species, at least throughout Italy (Bonelli, 1988). In the present study the 11.1 % of *P. fuscipennis* emerged in summer, before the removal of the sheaves. In fact, we found 87 cells in 16 nests (the 5.8 % of the cells) with empty cocoons. The cells with abandoned cocoons were the outermost, being constructed last. Only one nest was completely empty — all cells contained abandoned *P. fuscipennis* cocoons. Apparently a part of the studied population of the crabronid wasp gave rise to the so called “facultative generation”, while the rest of the offsprings was monovoltine.

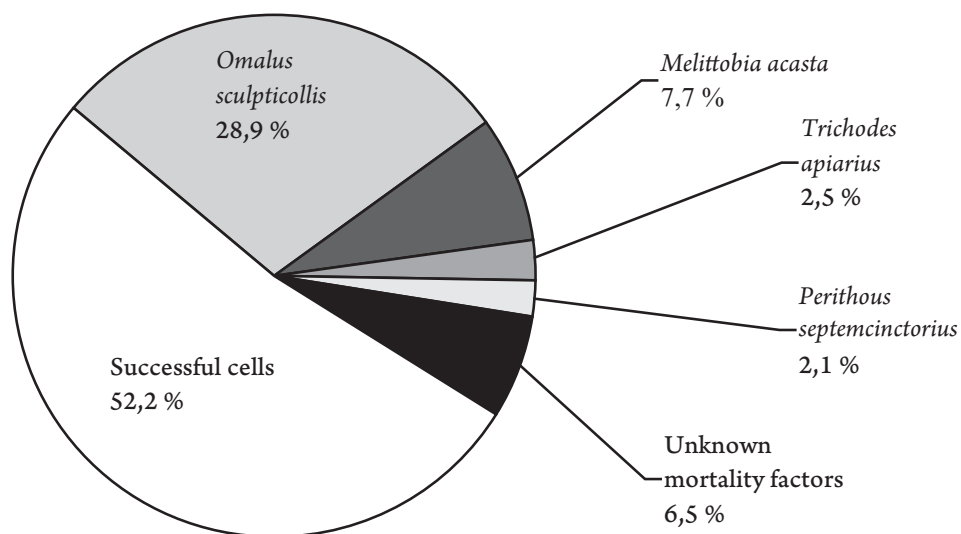


Fig. 2. Reproductive success and mortality of *Psenulus fuscipennis* progeny caused by different enemy species and other affects (in terms of number of cells).

Рис. 2. Репродуктивный успех и гибель потомства *Psenulus fuscipennis* от различных видов врагов и других факторов (в перерасчёте на количество ячеек).

Omalus sculpticollis Abeille, 1878

Taxonomical and morphological notes

The chrysidid wasp found in the *Psenulus* nests was identified as *Omalus* (*Chrysellampus*) *sculpticollis* Abeille, 1878 (Linsenmaier 1959 a, b, 1968, 1987, 1997). This species is easily identifiable for the unique punctuation of the mesosoma and the characteristic shape of the third tergite (fig. 3). *Omalus sculpticollis* was transferred into the genus *Philoctetes* Abeille, 1879 by Kimsey and Bohart (1991). Rosa and Soon (2013) also consider it belonging to the genus *Philoctetes*.

It should be noted that Linsenmaier divided the genus *Omalus* Panzer, 1801 into five subgenera: *Omalus* s. str., *Holophris* Mocsáry, 1890, *Philoctetes* Abeille, 1879, *Elampus* Spinola, 1806 (= *Notozus* Förster, 1853) and *Chrysellampus* Semenov-Tian-Shanskij, 1932, and placed *sculpticollis* in *Chrysellampus*. The Swiss author considered the original external morphological characters given by Abeille de Perrin to define the subgenus *Philoctetes*, as other authors did (Mocsáry, 1889; Radoszkowski, 1889; du Buysson, 1891; etc.). Kimsey and Bohart (1991), reviewing the tribe Elampini, considered different characters to identify the genera and elevated many subgenera to generic rank. The final result was that part of the former subgenera were elevated to genera, but with different diagnoses and species included, if compared to Linsenmaier's systematics. Therefore the genus *Philoctetes sensu* Linsenmaier is not comparable to *Philoctetes sensu* Kimsey, Bohart 1991. Some recent taxonomical publications demonstrated that Kimsey and Bohart's (1991) genera system needs corrections. Many taxa were recently moved from one genus *sensu* Kimsey, Bohart (1991) to other genera (Niehuis, 2001; Rosa, 2005 b, 2006, 2009; Strumia, 1995). However, Kimsey and Bohart's generic system is not accepted by many European and Russian authors (Kunz, 1994; Mingo, 1994; Vinokurov, 2008). A new revisional work on the Elampini tribe is needed. In the present paper we follow Linsenmaier's system (Linsenmaier, 1959 a, b, 1968, 1987, 1997).

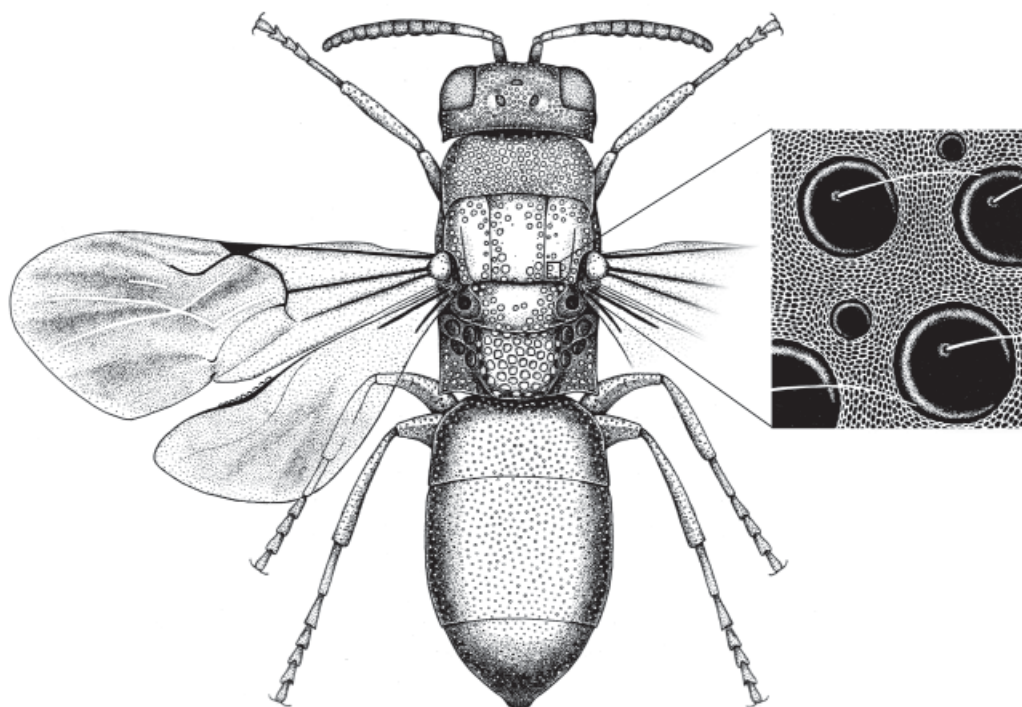


Fig. 3. *Omalus sculpticollis*, female, dorsal view and microsculpture of mesosoma.

Рис. 3. *Omalus sculpticollis*, самка, вид сверху и микроскульптура мезосомы.

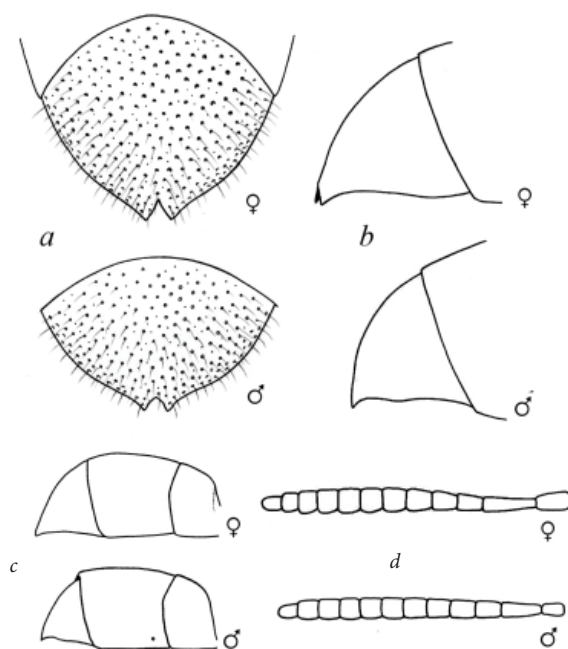


Fig. 4. Sexual dimorphism in *Omalus sculpticollis*: a — tergum III, top view; b — tergum III, side view; c — metasoma, side view; d — flagellum and pedicellum.

Рис. 4. Половой диморфизм у *Omalus sculpticollis*: a — тергит III, вид сверху; b — тергит III, вид сбоку; c — метасома, вид сбоку; d — жгутик и поворотный членик усика.

Du Buysson (1891) was the first author to observe the remarkable sexual dimorphism in *O. sculpticollis*: females have a more elongated metasoma and the third tergite (T-III) (fig. 4, b, c), the T-III is somehow protuberant (fig. 4, a, b), flagellomeres are swollen (fig. 4, d); seen in dorsal view, the males' head, main part of pronotum, mesonotum, propodeum, and upper part of metasoma are darker (matt black) (fig. 3). The matt effect on mesosoma in both sexes is originated from a special complex microsculpture, which could be named "coriaceous and punctate, with hairs" according to the terminology given by Eady (1968) (fig. 3). It should be noted that the coriaceous microsculpture preserves the structural coloration (except for black zones), but eliminates the iridescence effect in both sexes.

Summary of nest data

Only 90 specimens of *O. sculpticollis* emerged from the nests overall, but being the larvae they destroyed 435 cells of *P. fuscipennis* (see the discussion below). Therefore the common correlation "one parasitoid individual per one host cell" is not valid. At the moment of laboratory examination chrysidids were at prepupal or pupal stage, enclosed in cocoons, similarly to their hosts. As the examination took place early in spring (after winter stay) we can conclude that also *O. sculpticollis* overwinters in prepupal stage in the Crimea. The emergence of imagoes had been taking place from the second decade of May to the first days of June. But two of these 90 specimens emerged much earlier, during summertime: we observed one abandoned cocoon and one with dead imago. Therefore these two should be referred to the so called "facultative generation", and the studied population of *O. sculpticollis* could be considered as monovoltine.

Moreover, we can state the following: in the present study the 698 individuals of *P. fuscipennis* were monovoltine and emerged after winter stay, while other 87 (11.1 %) are referred to facultative generation; correspondingly, 88 individuals of *O. sculpticollis* were monovoltine, while two (2.2 %) emerged without winter stay (gave the facultative generation). These data prove a clear evidence of connection between the host's life cycle

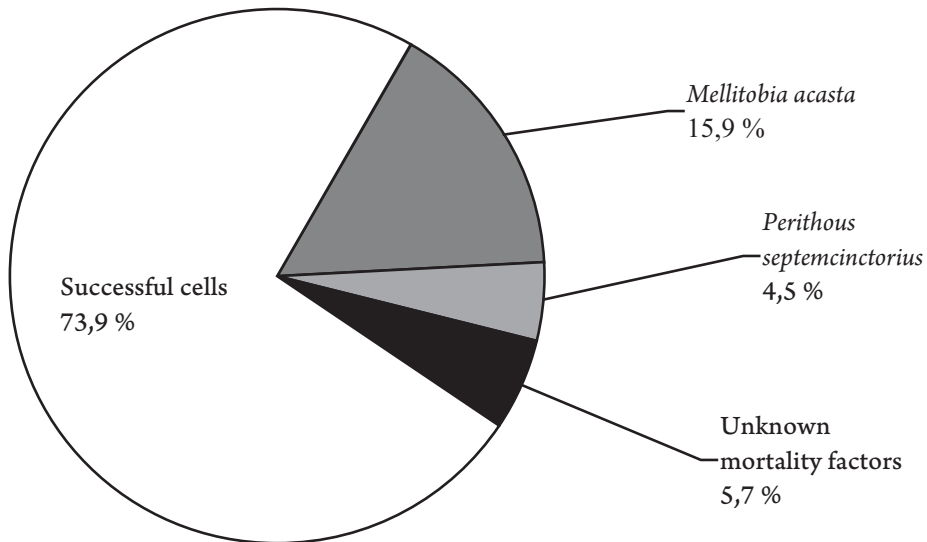


Fig. 5. Reproductive success and mortality of *Omalus sculpticollis* progeny caused by hyperparasites and unknown affects (in terms of number of cocoons).

Рис. 5. Репродуктивный успех и гибель потомства *Omalus sculpticollis* от гиперпаразитов и неизвестных причин (в перерасчете на количество коконов).

and its chrysidid enemy. In this sense the long-term evolution process becomes obvious, as the development of chrysidid wasp is synchronized with that of host (the dates of emergence are close and the facultative generations are shown in both host and chrysidid).

Not all *O. sculpticollis* successfully developed into imagoes. As shown in figure 5, the death of prepupae/pupae in cocoon was registered in five cases, 14 chrysidid cocoons were occupied by *Melittobia acasta*, four cocoons by the ichneumonoid *Perithous septemcinctorius*. In total, only the 73.9 % of *O. sculpticollis* emerged in about the same period, as the host. The sex ratio obtained for *O. sculpticollis* was almost 1 ♂ : 1 ♀.

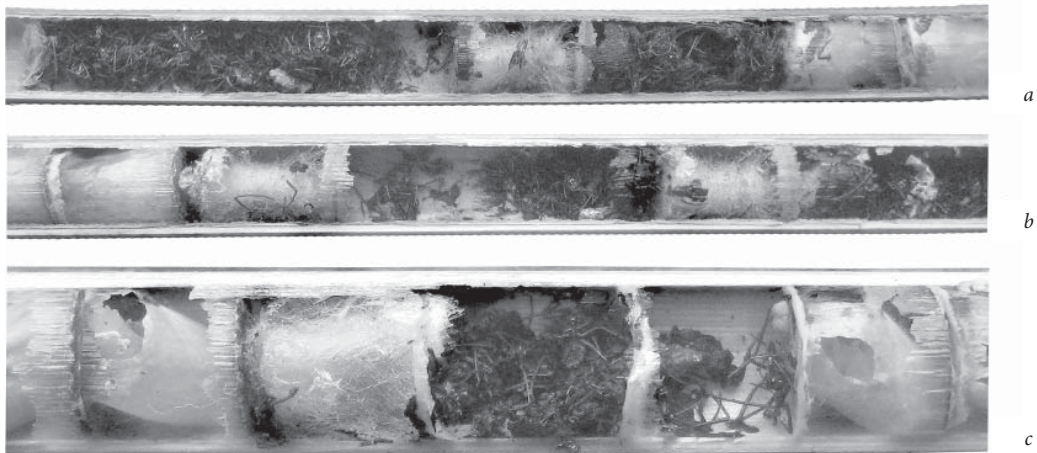


Fig. 6. Nests of *Psenulus fuscipennis* containing cocoons of *Omalus sculpticollis*: a — one chrysidid cocoon between mass of aphids and two host cells; b — two chrysidid cocoons, located after host cell; c — series of three cells, destroyed by chrysidid larva (note the cocoon in first cell and remainder of cell partitions with big holes).

Рис. 6. Гнёзда *Psenulus fuscipennis*, содержащие коконы *Omalus sculpticollis*: a — один кокон хризидиды среди массы тлей и две ячейки хозяина; b — два кокона хризидид, расположенные после ячейки хозяина; c — серия, состоящая из трёх ячеек, разрушенных личинкой хризидиды (см. кокон в первой ячейке и остатки перегородок между ячейками с большими отверстиями).

Omalus sculpticollis was found in 54 (56.8 %) of 95 nests constructed by *P. fuscipennis*. In each one of these 54 nests we observed that the series of intercellular partitions between the cells were damaged (fig. 6). The holes in the partitions were rather large, and the spaces of cells in such series appeared to be united. These united cells were always full of aphids and there was only one chrysidid cocoon always present per one series of cells (fig. 5). The series included from 2 to 14 cells (average — 5.0). In more than the 50 % of the cases, the nests contained two or three series of cells (respectively two or three *O. sculpticollis* cocoons per nest were obtained). The location pattern of these series in the nests of host was accidental — no regularity could be shown.

There are no doubts that this damage is caused by chrysidids. We did not find any other enemy inside the cell series as there were no extraneous holes found (which could explain the presence of other host enemies). These series were often situated in the “middle of the nest” being surrounded from both sides by cells with normally developing *P. fuscipennis*.

Though, one chrysidid wasp per one host cell was observed in seven cases on 90. Each such cell contained the cocoon of *O. sculpticollis* with prepupa/pupa inside and the remainder of an empty *P. fuscipennis* cocoon with a big hole (there were no aphids). All these facts indicate that chrysidid wasp devoured the mature larva of *P. fuscipennis*, which had already finished the feeding on aphids and spun its own cocoon. The hole in the host cocoon was made by the chrysidid larva.

Description of cocoon

The cocoon of *O. sculpticollis* looks like a brownish truncated cylinder with rounded posterior end (fig. 7). Its length can vary from 9 to 11 mm. The cocoon has a complex structure and consists of two parts, which differ in structure and functions.

The apical part consists of a transverse septum, made across the boring of the stem, and a circular band attached to it; the septum can include the remainder of intercellular partitions (constructed by *P. fuscipennis* female) on the periphery. All these structures resemble an “arch with collar” at the cross section of the cocoon (terminology by A. N. Kilimnik, pers. comm.). The collar is formed of the remainder of cell facing. The septum is made of opaque, rather thin, but quite dense yellowish material. A small depression is observed in the center of the septum. The circular band is much thinner, semitransparent, light-brown and it is often torn off during the removal of the cocoon. Functionally the arch serves as a plug or barrier, which separates the chrysidid larva from the mass of aphids and protects it from the superfluous humidity (Kilimnik, pers. comm.). The septum is not always attached to the remainder of cell partitions. When the cocoon is located out of relation to nest structure (in the middle of the cell or partially in one cell and partially in other), its arch could be less distinct, having more rounded forms, but still it preserves the functions.

The cocoon proper is thin-walled, varnished, light-brown, cylindrical with rounded ends (oval in cross section). Its apical part is inserted into the arch. The dense thick pubescence observed provides the junction of the cocoon and the circular band of the arch, which in turn fixes all the structures in the stem. The surface of the cocoon bears an abundant pubescence: it consists of thick brownish fibers all around the cocoon, except for the posterior end of the cocoon, where it is quite thin and whitish. According to Kilimnik (pers. comm.), the function of the pubescence is a shock-absorbing fixation of the cocoon to the nest walls. It should be noted, that the small inclusions (possibly excrements and chitinous remainder of host bodies) are observed within the pubescence all over. Excrements are black in color. Sometimes they can be described as the compact dense mass, arranged along the posterior part of the cocoon, otherwise they look like small round pellets laying more roughly. The apical part of the cocoon bears the nipple-like structure about 1 mm in diameter (fig. 7, c). The latter is well visible and distinctly

differs from the other semitransparent brownish parts of cocoon walls by being whitish and opaque. The minute examination of the nipple showed that it has a double-layer structure in cross section. The innermost lenticular layer is formed of very thin brownish fibers laying in parallel and compactly; instead the outermost one consists of more thick white fibers, laying loosely.

The emerging in linear nests forces the imagoes of chrysidids to get out of cocoons through their apical parts — by making holes first in the “nipple area” of the cocoon, and then in the transverse septum of the arch (fig. 7, *d*).

Sometimes the cocoons of *O. sculpticollis* have the inverted structure: the apical part bearing the nipple is not inserted into the arch, instead the bare nipple faces the entrance of the nest tube; additionally the arch is attached to the bottom end of the cocoon proper (fig. 7, *e*). Though such structure appeared to be reasonable, as it was revealed in the cases when the mass of aphids was situated behind the posterior part of the cocoon.

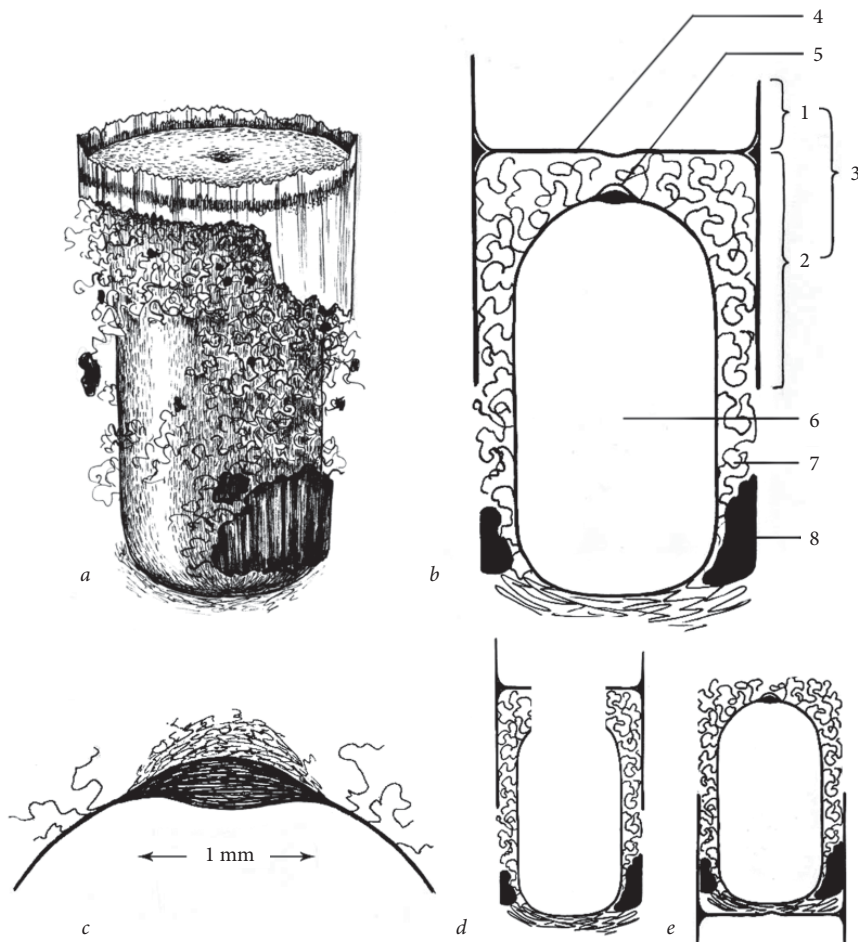


Fig. 7. Cocoon of *Omalus sculpticollis*: *a* — general view, part of circular band and excrements are removed; *b* — scheme of structure (1 — collar, 2 — circular band, 3 — arch, 4 — septum, 5 — nipple, 6 — cocoon proper, 7 — pubescence, 8 — excrements); *c* — cross section of nipple; *d* — scheme showing the cocoon after imago's going out; *e* — scheme of inverted position of arch.

Рис. 7. Кокон *Omalus sculpticollis*: *a* — общий вид, часть круговой полосы и экскрементов удалены; *b* — схема строения (1 — воротничок, 2 — круговая полоса, 3 — свод, 4 — перегородка, 5 — сосочек, 6 — собственно кокон, 7 — опушение, 8 — экскременты); *c* — поперечный срез через сосочек; *d* — схема, показывающая кокон после выхода имаго; *e* — схема инвертированного положения свода.

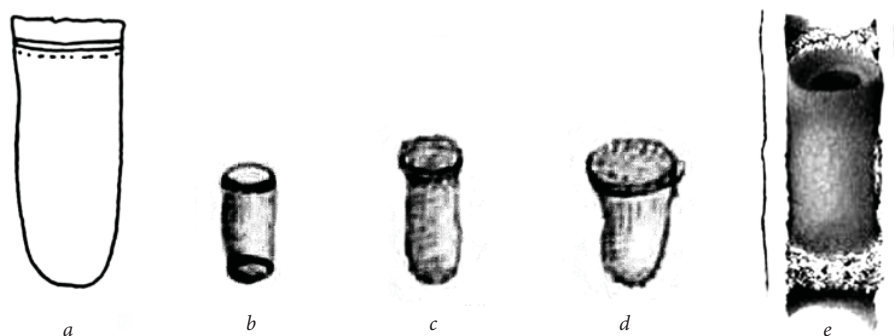


Fig. 8. Cocoons of the chrysidid wasps in the genus *Omalus*: a — *O. auratus* (from Danks, 1971); b — *O. pusillus*; c — *O. auratus*; d — *O. violaceus* (as *O. coeruleus*) (b, c, d — from Buysson, 1891); e — *Omalus* sp. (from Linsenmaier, 1972).

Рис. 8. Коконны представителей рода *Omalus*: a — *O. auratus* (по Danks, 1971); b — *O. pusillus*; c — *O. auratus*; d — *O. violaceus* (как *O. coeruleus*) (b, c, d — по: Buysson, 1891); e — *Omalus* sp. (по: Linsenmaier, 1972).

Analyzing the variation of *O. sculpticollis* cocoons, we can note the following: the wall thickness, size and coloration can vary considerably; the shape and the structure of the cocoon, the look and colour of the excrements, the presence of “nipple” and “arch” could be considered as stable features.

On the base of literature data (du Buysson, 1891; Maréchal, 1925; Grandi, 1959, 1961; Danks, 1971; Krombein, 1967) we can assume that the similar cocoon structure, as given above, is common for all the species in the genus *Omalus* Panzer, 1801 *sensu* Linsenmaier (fig. 8). Though the cocoon of *O. aeneus* (Fabricius, 1787), which is stored in the collection of the second author, differs from the cocoon of *O. sculpticollis* by having much more distinct nipple, which has also the membranous cap at the top, and by being smaller in size (length — 7 mm). According to detailed descriptions given by Grandi (1959, 1961) and Marechal (1925) the cocoon of *O. auratus* (Linnaeus, 1758) differs by the white to pale yellow color, the absence of distinct nipple (instead the wall of cocoon proper under arch is more dense, matt and opaque) and the smaller size too (length — 5 mm).

The larval features

The cocoons of *O. sculpticollis* contained the cast off skins of the last instar larvae. The level of sclerotization at mouthparts was high, and it was possible to identify some features of the mature larvae (fig. 9): coronal suture and parietal bands present; antennal orbits circular, located below the middle of head; labrum with depression in the middle and with almost strait apical margin; labrum and clypeus punctulate; mandibles fourdentate (symmetrical); maxillae and clypeus with strong, pigmented bands.

As the last instar larva of *O. auratus* was described in detail (Enslin, 1929; Giordani Soika, 1934; Grandi, 1959, 1961), it could be distinguished from that of *O. sculpticollis* at least by following: the labrum with six (3 + 3) sensillae in the anterior part, distinctly cutout in the middle; clypeus is trapezoidal. The mature larva of *O. aeneus* was also minutely described (Tormos et al., 1999). We can propose to differ it by emarginate labrum with six setae and six protuberant marginal sensillae and bidentate mandibles. The same is for *O. biaccinctus* (Buysson, 1891), which was studied by Tormos et al. (1996): its labrum is emarginate, with 10 short setae and six marginal sensillae, mandibles are tridentate. The drawings of head capsules given by Kilimnik (1993) provide the opportunity to differ the larvae of *O. pusillus* (Fabricius, 1804) at least by widely cutout labrum and the clypeus much bigger than labrum having the convex posterior margin; of *O. politus* (Buysson, 1887) by the presence of eight (4 + 4) sensillae on labrum and rugae on the lateral parts of clypeus (labrum is distinctly smaller than clypeus).

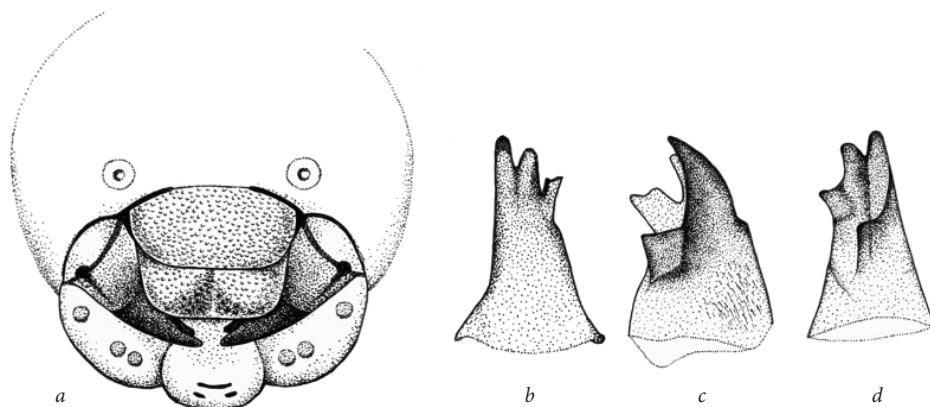


Fig. 9. Features of the last instar larva of *Omalus sculpticollis*: *a* — head, front view; *b-d* — left mandible (*b* — external side, *c* — top view, *d* — internal view).

Рис. 9. Особенности строения личинки последнего возраста *Omalus sculpticollis*: *a* — голова, вид спереди; *b-d* — левая мандибула (*b* — вид снаружи, *c* — вид сверху, *d* — вид изнутри).

Melittobia acasta Walker, 1839

Melittobia acasta overtook 7.7 % of *P. fuscipennis* cells and the pressure exerted on the host population is less considerable than the one exerted by *O. sculpticollis*.

M. acasta attacked also 14 cells (15.9 %) containing *O. sculpticollis* larvae. Consequently, *M. acasta* appeared to be parasitoid and hyperparasitoid at the same time for *P. fuscipennis* and *O. sculpticollis* correspondingly.

Perithous septemcinctorius (Thunberg, 1822)

Perithous septemcinctorius belongs to the subgenus *Hybomischos* Baltazar, 1961, which is sometimes treated as a valid genus name (Fitton et al., 1988). The species has a Holarctic distribution, and *P. fuscipennis* is already known as its host (Fitton et al., 1988). Additionally Aubert (1969) recorded it as a hymenopterous parasite for *Andricus* (Cynipidae), *Pemphredon*, *Psen*, *Psenulus* (Crabronidae) and listed *Omalus* as a possible host (Torgersen, 1972). The present study confirms Aubert's intuition. As in the case of *M. acasta*, *P. septemcinctorius* attacked both *P. fuscipennis* (2.1 % of cells) and *O. sculpticollis* (4.5 % of cocoons).

Trichodes apiarius (Linnaeus, 1758)

All the enemies of the host wasp discussed above are usually named “parasites in the broad sense or parasitoids”, while the beetles in the genus *Trichodes* could be considered as “nest destructors” (Zerova et al., 2006). In the present study they penetrated two nests and ruined 38 cells of *P. fuscipennis*. Nest destructors can cause huge damage in artificial nests, but in the present study they did not provoke considerable loss in the population of *P. fuscipennis*.

Discussion

An animal that is hunted by a predator is called prey or victim, in the case of a parasite it is called host. Hymenopterologists explained that the term “parasite” is out of use in

relation to wasps and bees. Many other terms have been proposed to describe the way of life of the preimaginal stages in the so-called parasitic Hymenoptera: parasitoid, cleptoparasite, brood parasitoid (inquiline in Russian literature), social parasite, carnivoroid (Parker, 1936; Iwata, 1976; Malyshev, 1966; Krombein, 1967; Tormos et al., 1996; Tobias, 2004). But the term “host” is still widely used, especially in discussions on the biology of Chrysididae. The food supply for Chrysidid larvae is ensured by the progeny of their host or by their prey stored by the adult female; the shelter is provided by the host adult females (cells and nest) or its mature larvae (cocoon); the protection from enemies is given by special nest structures. Consequently the term “host” could not be apprehended from the standpoint of food supply only. For example, Bonelli (1988) observed that the females of *P. fuscipennis* can remain in their nests for a long time, till their natural death, defending them against enemies. We observed dead females in some nest tubes (near the closing plug), partially overtaken by chrysidids.

It is important, while detecting the new host-parasitoid relationships in Chrysididae, to name exactly the food resource of larvae (if it is possible) and to make observations on their habits. Such data can help to consider all the variety of chrysidids' behavior at immature stages.

Malyshev (1966) attributed the family Chrysididae to the “wasp-like (bethiloid) phase”. He considered the chrysidids to be inquilines, metaparasites or orthoparasites depending on the feeding habits of their larvae. Inquilines feed on the provisions stored by the adults intentionally killing the egg or the young larva of the host or leaving it for starvation death. In this sense the term “inquiline” corresponds to “brood parasitoid” *sensu* O'Neill (2001, as a specialized form of cleptoparasitism). Metaparasites, or delayed parasites, being laid in a cell where the host is only an egg, wait till the latter becomes a mature larva and only then quickly devour it. Orthoparasites, or direct parasites, are laid on prepupae or pupae, which will be soon consumed. Following Kilimnik (1993), we consider such division to be quite useful.

Apparently species in the genus *Omalus sensu* Linsenmaier attack crabronid wasps in the subfamilies Pemphredoninae and Philanthinae (Berland, Bernard, 1938; Kilimnik, 1993; Rosa, 2006). As far as we know, there are only two records on the biology of *O. sculpticollis*: Abeille de Perrin found one specimen in the nest of *Pemphredon rugifer* Dahlbom, 1844 (as *Cemonus unicolor* Fabricius) (Buysson, 1891; Bohart, Menke, 1976); Kilimnik (1993) reported the ground-nesting wasp *Diodontus major* Kohl, 1901 as the host of this species. In the present study another crabronid wasp, *P. fuscipennis*, is proved to be the host of *O. sculpticollis*.

The obtained data indicate that the larvae of studied chrysidid can destroy more than one host cell searching for food (up to 14 cells). The same fact had been previously reported by Danks (1971) for *Omalus* (s. str.) *auratus* (Linnaeus, 1758) obtained from the nests of *Pemphredon lethifer* (Shuckard, 1837). The ability of the young larva of *O. sculpticollis* to destroy the partitions in the host nests seems to be questionable. Therewith some questions arise: why does the chrysidid larva leave the cells full of aphids which can cause bacterial and fungi infections? Why does it spend energies for braking the nest partitions and then for reconstruction an analogue one in its own cocoon? We can argue that:

1. The partitions in the nests of *P. fuscipennis* are very thin membranous diaphragms, as described by Malyshev (1966) and Bonelli (1988). They are formed of two silky layers, which face all the cell walls. Consequently, if the young chrysidid larva is able to bite through the integument of the host larvae or egg, it might be able to damage the thin partitions in the nest.

2. Most probably it is the second or third instar larva which destroys the partitions in the host nest. Tsuneki (1952) and Kilimnik (1993) observed that the newly hatched larvae of *Omalus* first eat one or a couple of aphids stored in the cell, and then seek

for and devour the larvae of their host. Kilimnik proposed to name such peculiarity in the development of the first instar larvae of chrysidids as “facultative inquilinism” (because the following development of chrysidid larvae corresponds to other type of feeding habits). Subsequently, we suppose that the newly hatched larva of *O. sculpticollis* first feeds on the contents of one cell, and after the first or second molt it destroys the partitions penetrating into other cells.

3. *O. sculpticollis* larvae feed on *P. fuscipennis* progeny, but not on aphids. The evidence is given by the number of aphids found in the cells destroyed by *O. sculpticollis*. Additionally the presence of seven *O. sculpticollis* cocoons, each inside the cocoon of *P. fuscipennis*, indicates that chrysidid larvae fed on host exactly. Accepting such assumptions, we can explain other aspects. The number of cells destroyed by the chrysidid larva could be connected with the level of maturity of the host larvae. The nest of *P. fuscipennis* can contain prepupae/pupae inside the cocoons, mature larvae and feeding larvae of different ages at the same time (Bonelli, 1988). Hatching in the cell where the host had reached almost maximal weight or already began to spin the cocoon, provides the chrysidid larva with all needed resources. On the other hand, if *O. sculpticollis* larva had hatched in the cell where the host is only a young larva or even an egg, it is forced to seek for needed resource (see below) in other cells, leaving behind all the stored aphids.

4. The chrysidid larvae can be the “hormonal parasites” (V. V. Martynov, pers. com.): we can assume that the bodies of *P. fuscipennis* larvae, which are subjected to germination, provide young chrysidids not only with organic substances to be digested, but with a portion of larval hormones. The advanced mature larvae provide chrysidids with needed resources — there is no need for the latter to penetrate other cells. We should note that observations of the development of immature stages of chrysidids in the genus *Omalus* are rather scanty. Only a couple of studies could be compared. Tsuneki (1952) observed the development of *Omalus* (s. str.) *auratus* Linnaeus, 1758 larvae, which devoured the young larvae of *Pemphredon rugifer* Dahlbom, 1844 (as *P. unicolor* Panzer) after the facultative feeding on aphids and then successfully finished feeding on aphids stored in the cell. As these observations were made on the material transferred to glass vials we cannot be sure that the development of chrysidids *in vivo* does not differ in some way. Though Grandi (1959, 1961) reported the same behavior of this species. Danks (1971), while reporting that *O. auratus* feed primarily on the provisions, added that one individual may destroy more than one host cell. Consequently a question arises, if the cells are destroyed seeking for aphids, which can represent the food for chrysidid larvae, or the situation with cells is similar to those discussed in the present study (chrysidids feed on host larvae), considering that Danks’s phrase “feeding primarily on the food store” is not really clear. The study of the latter author, as well as the other (Berland, Bernard, 1938; Rosa, 2006), showed *O. auratus* to be the enemy of aphid-, spider- and fly-storing hosts (in the genera *Pemphredon*, *Passaloecus*, *Trypoxylon* and *Rhopalum*). It seems more probable, that *O. auratus* feeds on the host progeny (attacking the wide range of wasps in the family Crabronidae), than on a various food store. Nevertheless, the host-parasitoid relationship between *P. fuscipennis* and *O. sculpticollis* confirm Kilimnik’s conclusion: immature stages of wasps in the genus *Omalus* sensu Linsenmaier feed on host progeny, and only their first instar larva can eat a small amount of stored insects (being a facultative inquiline).

The studied *O. sculpticollis* specimens could not be regarded as inquilines (except for the peculiar development of first instar larva), as it is discussed above. Considering the location of the invaded cells in *P. fuscipennis* nests, the only possible way for the adult chrysidids to enter these cells was during the nest construction. Consequently it cannot belong to orthoparasites, whose adults penetrate when the cells are finished. Metaparasites “get” the ability to feed on full-grown larvae due to the asynchrony in the development with the host progeny. As it was already observed for some species of the genus *Chrysis*

(*Chrysogona*) Linnaeus, 1767 attacking solitary bees, the chrysidid larva hatches about at the same time as the host, but it remains as a first instar larva till the bee larva becomes mature and begins to spin its cocoon; during all this time the young chrysidid larva appears to be attached to the bee larva by its mandibles (Ferton, 1905; Krombein, 1967). In this sense *O. sculpticollis* could not be called metaparasite, as the waiting stage is absent and the rate of asynchrony in the development of the species and its host is not the same for all individuals. Apparently, the difference in developmental speed of host larvae is so big, that each newly hatched chrysidid larva can get different supply conditions. As it is said above, the hatching in the cell where the host larva reached maturity can provide enemy with all needed resources: it is enough for *O. sculpticollis* to get into one cocoon of *P. fuscipennis*. In the case, when the host is a young larva, the chrysidid penetrates into other cells searching for new victims acting like a predator. Here we can find one more difference in behavioral pattern with typical metaparasites: *O. sculpticollis* does not “wait” passively for host maturity, but takes an active position ruining the cells. In this sense the term “carnivoroid” introduced by Malyshev in 1964 (Tobias, 2007) to underline the predatory habits of larvae of entomophagous Hymenoptera seems to be quite appropriate. Considering, that Tobias (2004, 2007) examining deeply the problem of terminology in this group, proposed to apply the term “parasitoid” to endoparasites, and “carnivoroid” — to ectoparasites, we can conclude, that larva of *O. sculpticollis* acts as carnivoroid in relation to progeny of *P. fuscipennis*.

Turning once more to classification introduced by Malyshev, we can suppose that if the revealed host-parasitoid relationship does not fall under any of three behavioral patterns previously attributed to chrysidids (inquilines, metaparasites, orthoparasites), it belongs to other, undeclared one. We can note that the main feature of “such carnivoroids” is the ability to compensate the lack of resources, which can be found in one host cell, by penetration into other cells. We can propose to name chrysidids with life history analogous to *O. sculpticollis* the reptoparasites (from Latin “repto” — to crawl over, to pass through), underling their ability to move inside the host nest.

Conclusions

1. *Omalus sculpticollis* is a specialized entomophagous insect; its larva acts like a carnivoroid devouring the progeny of *Psenulus fuscipennis*; one larva can attack more than one host cell (up to 14); the cocoon has the special structure, which increases the chances for survival in the host nest; by the special life history of preimaginal stages the species must be attributed to the separate behavioral group — we suggest to name such chrysidids “the reptoparasites”.

2. The chrysidid wasp is the most important regulator within the Crimean population of *P. fuscipennis* compared to the other enemies: *Melittobia acasta*, *Trichodes apiarius*, and *Perithous septemcinctorius*. *Melittobia acasta* and *P. septemcinctorius* attacked both progenies of *P. fuscipennis* and *O. sculpticollis*, and they can be considered as hyperparasites.

3. The degree of synchrony in the development of the chrysidid wasp and the crabronid wasp is rather high: the oviposition and adults’ emergence are simultaneous. Both *O. sculpticollis* and *P. fuscipennis* are monovoltine, having small facultative generations.

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