Acta entomologica serbica, 1999, 4 (1/2): 107-125 UDC 595.792.17

MORPHOLOGICAL ADAPTATIONS OF THE OVIPOSITOR OF BRACONID WASPS (BRACONIDAE : HYMENOPTERA) ASSOCIATED TO BIOLOGICAL CHARACTERISTICS OF THEIR HOSTS

M. Brajković, M. Krunić, Ž. Tomanović and Lj. Stanisavljević

Institute of Zoology, Faculty of Biology, University of Belgrade,
Studentski trg 16, YU-11000 Belgrade

Ovipositor structure of species belonging to 21 braconid subfamilies has been analyzed. Changes in the complex of genital plates and valves occurring during braconid adaptation to parasitization of their hosts have been observed. A special attention has been paid to changes in the ovipositor structure in braconids adapted to lay eggs into the eggs and adult of the host.

Key Words: Braconidae, ovipositor, hosts, adaptations.

INTRODUCTION

Braconidae are one of the greatest insect families belonging to the order of hymenopteres. About 15,000 braconid species are known to date, but there are probably 40,000 species (Matthews, 1974). Although numerous and widespread, they are little investigated. The braconids are primary parasites of other insects (Papp, 1974). Most braconids parasitize species from holometabolous orders, primarily Coleoptera, Lepidoptera, Diptera, Hymenoptera and Neuroptera, while a few species parasitize hemimetabolous insects of Heteroptera, Homoptera, Psocoptera and Isoptera. In braconid life cycle it is larva that lives as a parasite, while imago lives freely, usually for a short time feeding on nectar. Phytophagous species, i.e. species whose larvae develop in plant tissue feeding on it, have recently been discovered among braconids (Marsh, 1991). This is a very important finding which has questioned all assumptions on phylogenetic place of braconids in the division of Parasitica of Hymenoptera order, i.e.

on them as a group originating from other Parasitica.

Two groups of parasites, endoparasites and endoparasites, have developed during phylogeny of braconids (TOBIAS, 1967, ACHTERBERG, 1984). Ectoparasites are phylogenetically older braconids. Endoparasitic braconids which are much more numerous developed later while the phytophagous ones are probably the youngest. Ectoparasitic braconids are characterized by laying eggs in larvae of Coleoptera, Lepidoptera, Hymenoptera and Diptera. From the laid eggs develop larvae feeding on the host body and the final effect is the death of the host larva making, from the ecological point of view, parasitoids more proper name for them. The females of ectoparasitic braconids while laying eggs paralyse host larva permanently with secretions injected by alkaline and acid glands through the ovipositor. The host larva stays alive but immobile during the whole development of the parasite. The females of species parasitizing concealed larvae , i.e. hosts that live in tree, under the bark, in the leaf or in galae while laying eggs first bore the substrate in which the host lives so that their ovipositor has three functions: probing the substrate, piercing integument of the host, paralyzing the host and laying eggs. Ectoparasitic braconids have a narrower spectrum of hosts because they parasitize larvae of four orders of holometabolous insects, but most species are polyphagous, i.e. infest and develop on larvae of several species belonging to the orders of Coleoptera, Lepidoptera, Hymenoptera and Diptera, while some parasitize species belonging to all the mentioned orders. Infestation of host eggs in this group is rare (ROHWER, 1925).

Endoparasitic braconids lay eggs into the host body paralyzing it temporarily with secretions of ovipositor glands. Endoparasitic braconids are much more numerous and their array of hosts is wider encompassing both holometabolous and hemimetabolous insects. Endoparasitic braconids have not only a wider array of hosts but also developed in addition to larval parasitism as a dominant form of parasitism egg-larval and imaginal forms of parasitism. Widening of the spectrum of hosts and stages is accompanied with specialization for parasitizing fewer number of host species (oligophagia). Some endoparasistic braconids are monophagous, i.e. found to date to parasitize only one host species. Polyphagia is according to many entomologists plesiomorphic characteristic, the general trend in evolution being towards monophagia.

During long-lasting evolution and adaptation to various forms of parasitism within braconids many changes occurred in morphology, larval and imago structures. Considerably great, if not the greatest changes occurred in anatomy and morphology of the ovipositor.

The objective of this paper is to analyse changes in ovipositor structure of braconids which took place during adaptation to parasitization to different hosts.

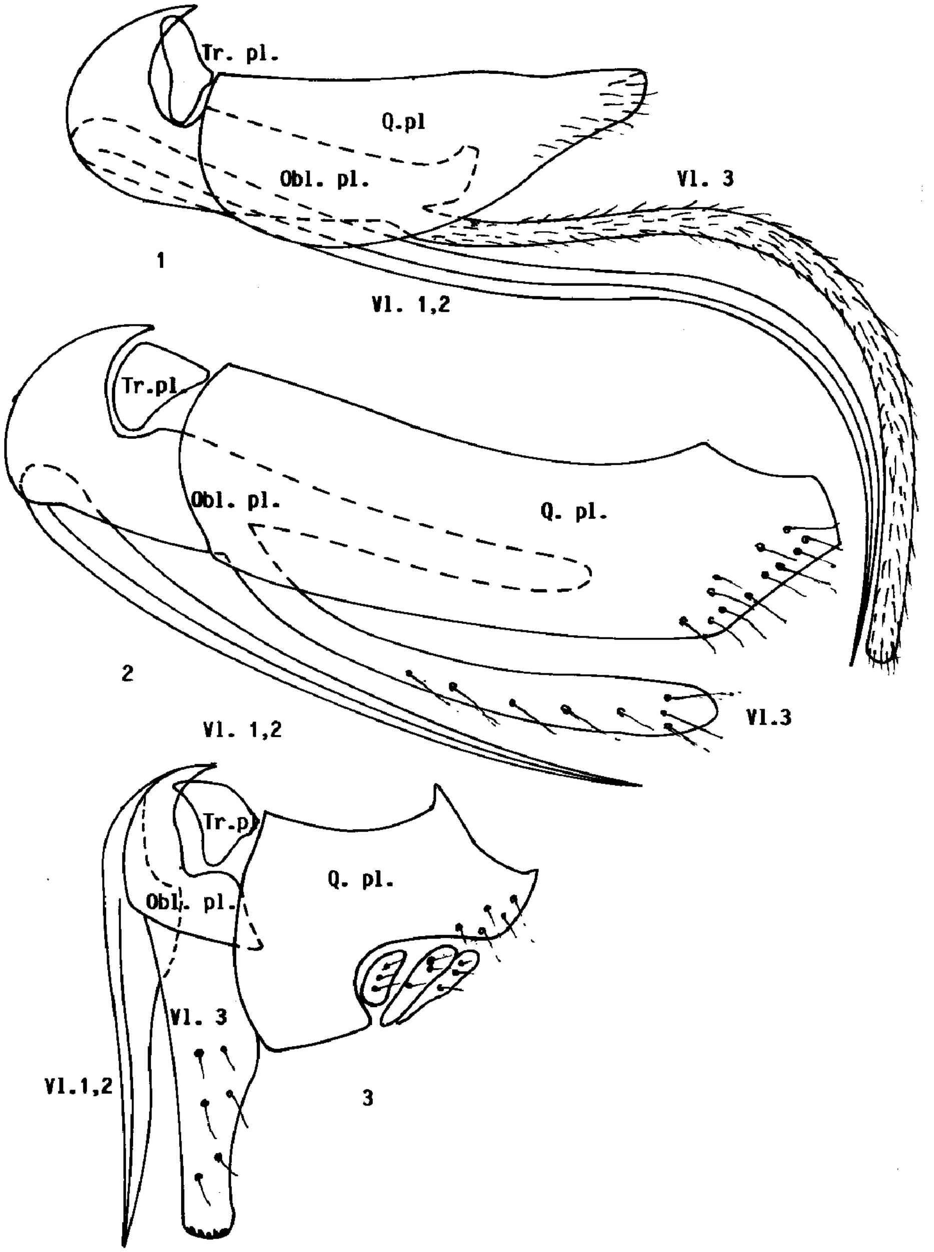
MATERIAL AND METHODS

To study the ovipositor structure the species from the following subfamilies and species have been selected: Doryctinae, Braconinae, Rogadinae, Helconinae, Macrocentrinae, Agathidinae, Orgilinae, Microgasterinae, Homolobinae, Sigalphinae, Cardiochilinae, Cheloninae, Adeliinae, Brachistinae, Ypsistocerinae, Alysiinae, Opiinae, Ichneutinae, Euphorinae, Aphidiinae and Hybrizontinae. The ovipositors were taken out of abdomen, then degreased in KOH, dehydrated in a series of alcohol. From 100% alcohol it was put into tholuol and then mounted on microscope slides. A lateral view of the ovipositor is given in all figures while only in figures 22 and 23 was given a ventral view of the ovipositor. We have used the braconid classification after ACHTERBERG (1976), TOBIAS *et al.*, (1986) and MARSH *et al.*, (1987), while Aphidiinae and Hybrizontinae have been added since some authors include them into braconids.

RESULTS AND DISCUSSION

The ovipositor of braconids is a complex morphological, anatomical and functional structure. Disregarding the origin of this structure, it has common general pattern. (Figs. 1, 2 and 3). The skeletal part of the ovipositor is made up of three pairs of plates and valves. Muscles are attached to these parts. Canals of acid and alkaline glands and final part of reproductive system (vagina and egg canal) are connected to the ovipositor. The base of the ovipositor is made up of the triangular, quadrate and oblong plates. Complex musculature is attached to them enabling the ovipositor to function. To the fore end of this complex with rami are connected valves I and II which make a structure by which braconids bore substrate or the integument of the host, inject poisonous secretions and lay eggs. Valves III are connected to oblong plates and in some braconids hold valves I and II at laying the eggs while in other they lose this function and only serve as sensory organs or have some other functions.

Parasitism in braconids had a tumultuous evolution during which over thirty taxa in the rank of subfamily with probably over 40,000 species developed (TOBIAS, 1967; MATTHEWS, 1974; PAPP, 1974; MARSH, 1979; ACHTERBERG, 1976, 1993).



Figs. 1-3; 1. *Hdomolobus* sp. (Hornolobinae), 2. *Hlibrizon buccata* Breb. (Hibrizontinae), 3. *Aphidus ervi* Hal. (Aphidiinae). Tr. pl. = triangular plate, Obl. pl. = oblong plate, Q. pl. quadrat plate, Vl. 1,2 = first and second valvae, Vl. 3 =third valvae.

Ectoparasitic braconids encompass subfamilies Doryctinae and Braconinae. ACHTERBERG (1993) within ectoparasitic braconids finds also Horminae, Lysiterminae, Pambolinae and Rhyssalinae. Some authors exclude Exotecinae from Braconinae (MARSH, 1979). For some subfamilies as Khoikhoinae, Vaepelinae, Pselaphaninae, Histeromerinae, Apozyginae, Trachipetinae and Telengainae it is still unknown if they are ectoparasitic or endoparasitic ones. A conspicuous morphological trait of imago of ectoparasitic braconids is clypeus deeply emarginate (open mouth). Doryctinae are traditionally considered the most primitive ectoparasitic braconids, but recent finding of phytophagous species in Brasil (MARSH, 1991) belonging to doryctines questions this and supports Tobias'opinion (1981) that divergence within the family Braconidae started at the same time in over 30 directions.

The most primitive ectoparasitic braconids parasitize concealed larvae of Coleoptera. The females of these braconids at oviposition after locating the host larva bore substrate (bark, tree) with the valves I and II. Oviposition in this case lasts in some braconids for only thirty minutes (MARSH, 1965). At this stage of oviposition serrations on the first valves (in most genera being over ten in number, the most numerous (19) being found in genera *Leluthia* and *Megaloproctus* Fig. 4) are of special importance. Valves III at oviposition give support to the valves I and II. The genital plates are elongated, especially quadrate and oblong ones connected the muscles to the valves I and II thus enabling movements of the valves I and II and successful boring of the substrate. The valves III in ectoparasitic braconids are linked to distal parts of oblong plates giving the maximum support to valves I and II at oviposition since the longer the lever the stronger the support (Figs. 4, 5, 6). Within ectoparasitic braconids there is a clearly pronounced tendency of infestation of the nonconcealed host larvae, larvae of younger stages (I and II) or the larvae living shallowly buried in plant tissue such as leaf mining. In these braconids the ovipositor shortens as well as the complex of genital plates, teeth and all three pairs of valves. Shortening of these structures is followed by reduction of teeth at the tip of the valves I and II because there is hardly any need for boring. A very illustrative example of the ovipositor with this feature is met in some species of the genera *Hormius*, *Bracon* (Fig.5) and *Hormica* (Fig. 6).

The structure of the ovipositor of ectoparasitic braconids varies considerably, but on the basis of this structure it is possible to estimate phylogenetic relationships between taxa.

Endoparasitic braconids are much more numerous than the ectoparasitic ones. The spectrum of their hosts is much wider and, as mentioned earlier, includes holometabolous and hemimetabolous insects. In contrast, they have a very pronounced tendency to specialize for parasitizing certain species, i.e. tendency towards monophagia.

A transitional group between ectoparasitic and endoparasitic braconids is *Rogadinae*. They, like ectoparasitic braconids, have a developed circular opening, but the females lay eggs in uncovered caterpillars of butterfly they temporarily paralyze. A complete development and pupation takes place in caterpillars. The ovipositor of rogadines is short (Fig. 7), i.e. plates are short and wide, valves I have few serrations (*Cystomastax* and *Pelecystoma* (Fig. 8) have 6-7 serrations, some species of *Rogas* have 4-5, while a considerable number of them are toothless). Valves III are shortened and wider and connected to the hind half of the oblong plates giving no support to stylet as they serve only as sensory organs.

Endoparasitic braconids include the following traditionally established subfamilies: Helconinae, Macrocentrinae, Agathidinae, Homolobinae, Opiinae, Alysiinae, Microgasterinae, Cardiochilinae, Miracinae, Sigalphinae, Cheloninae, Ypsistocerinae, Adeliinae, Brachistinae (Calyptinae), Orgilinae, Neoneurinae, Euphorinae, Aphidiinae and Hybrizontinae. The spectrum of hosts parasitized by endoparasitic braconids is much wider than the one parasitized by ectoparasitic braconids. Widening of the host spectrum is followed by specialization to parasitize certain groups. The species of the subfamilies Macrocentrinae, Microgasterinae, Agathidinae, Cheloninae, Sigalphinae, Adeliinae, Cardiochilinae, Miracinae and Orgilinae parasitize caterpillars; Helconinae parasitize concealed larvae of Coleopterae, whereas species of the subfamilies Alysiinae and Opiinae parasitize only larvae of Diptera, while Aphidiinae parasitize nymphs and adults of aphids.

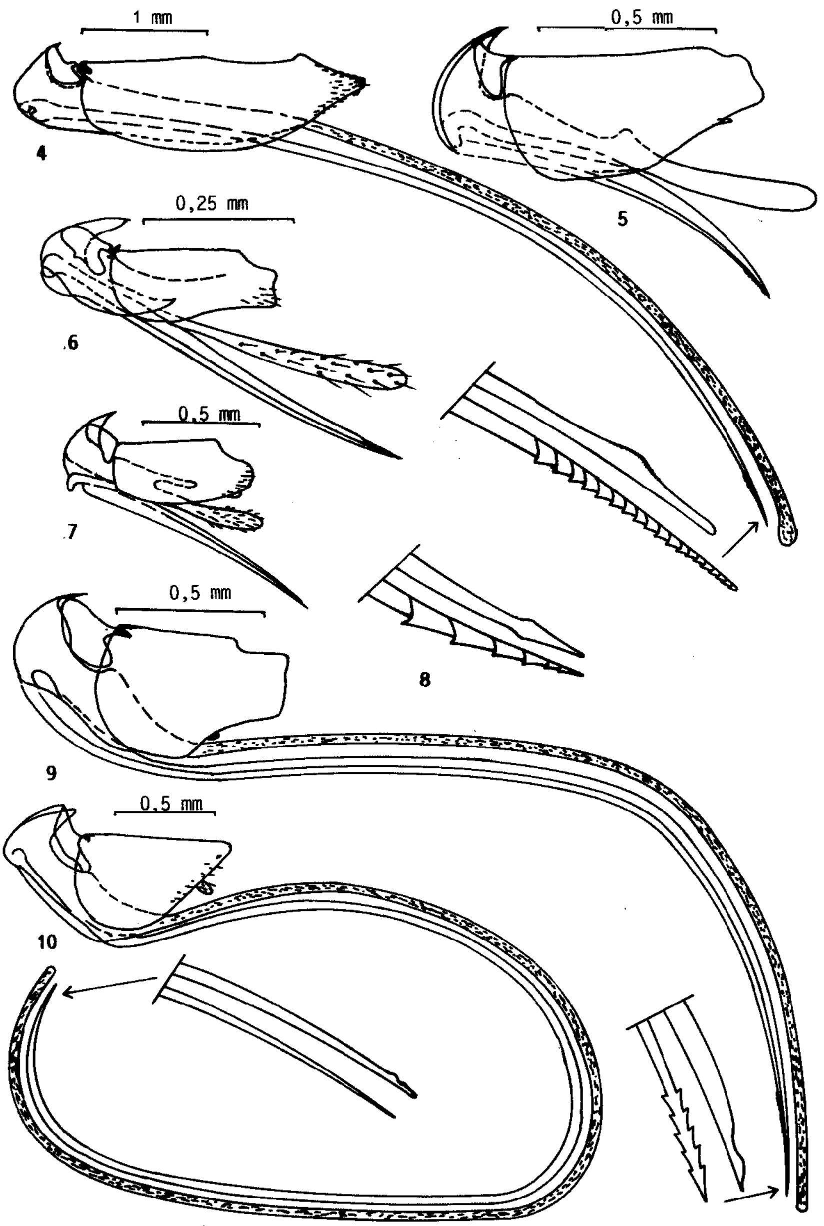
Within endoparasitic braconids two new forms of parasitism developed: egg-larval and imaginal one as, it seems, highest forms of parasitism within this group. A dominant and ancestral form of parasitism is without any doubt larval parasitism. Endoparasitic broconids when laying eggs into host larva bore body wall of the larva by the tips of valves I and II and inject secretions of poison glands to paralyze it temporarily. The oviposition in endoparasitic braconids is in comparison to that in ectoparasitic ones much quicker because there is hardly any need to bore the substrate. In some it is, as a rule, a thin plant tissue easy to drill. Their eggs are smaller and pass through the ovipositor canal (which is also shorter) much more easily .

According to some authors the subfamily Helconinae belongs to the most primitive endoparasitic braconids. Imagoes are quite large, females have long ovipositor which they push into tunnels where concealed larvae of Coleoptera (Cerambycidae, Bostrichidae, Buprestidae, Scolytidae, Curculionidae, Anobiidae, Chrysomelidae) live (Fig. 9). Due to this type of oviposition in the species of this subfamily (*Helcon, Wroughtonia, Cenocoelius* and *Diospilus*) valves are very long and are 5 to 6 times the length of the complex of genital plates. Valves I carry 4 teeth on their tip. It seems that they pierce plugs made by host larvae.

In the body size and ovipositor structure helconines are very similar to the subfamily Macrocentrinae (Fig. 10). They are solitary or gregarious parasites of the caterpillars from the families Noctuidae, Nymphalidae, Lymantridae, Coleophoridae, Gelechidae, Geometridae, Phycitidae, Tortricidae, Oecophoridae and probably from the families closely related to them. The complex of genital plates of the ovipositor of the genera *Macrocentrus* is short, while valves are very long being 8-9 times the length of the complex of genital plates. Valves I are toothless, while valves II have a small hole preventing stylet to come out from the host body at oviposition (Fig. 10, tips of stylets). The long ovipositor is an adaptation to the act of oviposition since the females pierce the caterpillars from quite a distance although they are at the same time much larger than females (Fink, 1926, Haeussler, 1932). In some cases the ovipositor should drill the substrate in which the host larvae live (Parker, 1931).

Agathidinae are in biology similar to macrocentrines because they parasitize caterpillars from several families, most frequently from Tortricidae, Gelechidae, Pieridae, Oecophoridae, Coleophoridae, Geometridae and Noctuidae (Stultz, 1954; Zlatanova, 1970; Bacht & Gupta, 1977). Adults from this subfamily are remarkably different from those of other braconids by elongated downward head and labio-maxillar complex. An interesting trait Agathidine may always be recognized by is very long and backward curved fore apexes of the oblong plates and very narrow triangular plates (Fig. 11). The function of these structures is unknown for the moment. As for valves, they are fairly long, 3-5 times longer than the complex of the genital plates. Dentations on valves I are almost completely reduced.

In morphology and biology these two subfamilies are apparently very close to Orgilinae with the genera *Orgilus*, *Microtypus* and *Charmon*. They are also relatively large wasps parasitizing caterpillars of Tortricidae, Oecophoridae, Coleophoridae, Gelechidae, Noctuidae, Phycitidae and Psychidae (Oatman *et al.*, 1961). The ovipositior of these species is characterized by fairly long valves (3-5 times longer than the complex of genital plates) (Fig. 12). Such valves serve to lay eggs into larvae which live in tunnels or leaf miners. Valves I have small teeth or completely reduced teeth



Figs. 4-10; 4. *Mlegaloproctus* sp. (Dorycyinae), 5. *Bracon gastroidae* Ashrn. (Braconinae), 6. *Hormisca tatianae* Tel. (Exotecinae), 7. *Rogas stigmator* (Say) (Rogadinae), 8. *Cystomastax theretre* (tip of the first and second valvae) (Rogadinae), 9. *Helcon pedalis* Cress. (HeIconinae), 10. *Macrocentrus thoracicus* Nees (Macrocentrinae).

whereas valves II have a hole at the tip which obviously serves to prevent stylet to come out from the caterpillar body at oviposition because, as well-known, the caterpillar fights moving the whole body when pierced by a parasite.

Very close to the mentioned subfamilies are Homolobinae (Fig. 1), and Sigalphinae which also parasitize caterpillars. Among them a clear tendency towards ovipositor shortening is seen as a consequence of adaptation for laying eggs into juvenile caterpillars. This makes them in biology close to the subfamilies Microgasterinae, Cardiochilinae and Miracinae whose spiecies also parasitize caterpillars (Chamberlin & Tenth, 1926; Muesebeck, 1937; Vance, 1932; Hafez, 1951; Allen, 1958; Osmolovsky, 1964; Cardona & Oatman, 1971). Within this large group of braconids an egg-larval parasitism stemmed up. (Tadić, 1959; Wilbert, 1960). The ovipositor of these braconids varies from long with an elongated complex of genital plates met in some species of *Apanteles* (Fig. 13) to the very short one with wide complex of genital plates, short valves I and II, and valves III moved foreward as in the genera *Cotesia* (Fig.14) and *Cardiochiles* (Fig. 16). Within the group there are fine transitions between the extremes mentioned. All these changes are related to the process of adaptation to parasitizing free and juvenile caterpillars. Very interesting changes are met in valves III in the species of the genus *Protomicroplitis* (Fig. 15) which on their tips have a row of large, short bristles used to hold caterpillars or lean against the ground during oviposition.

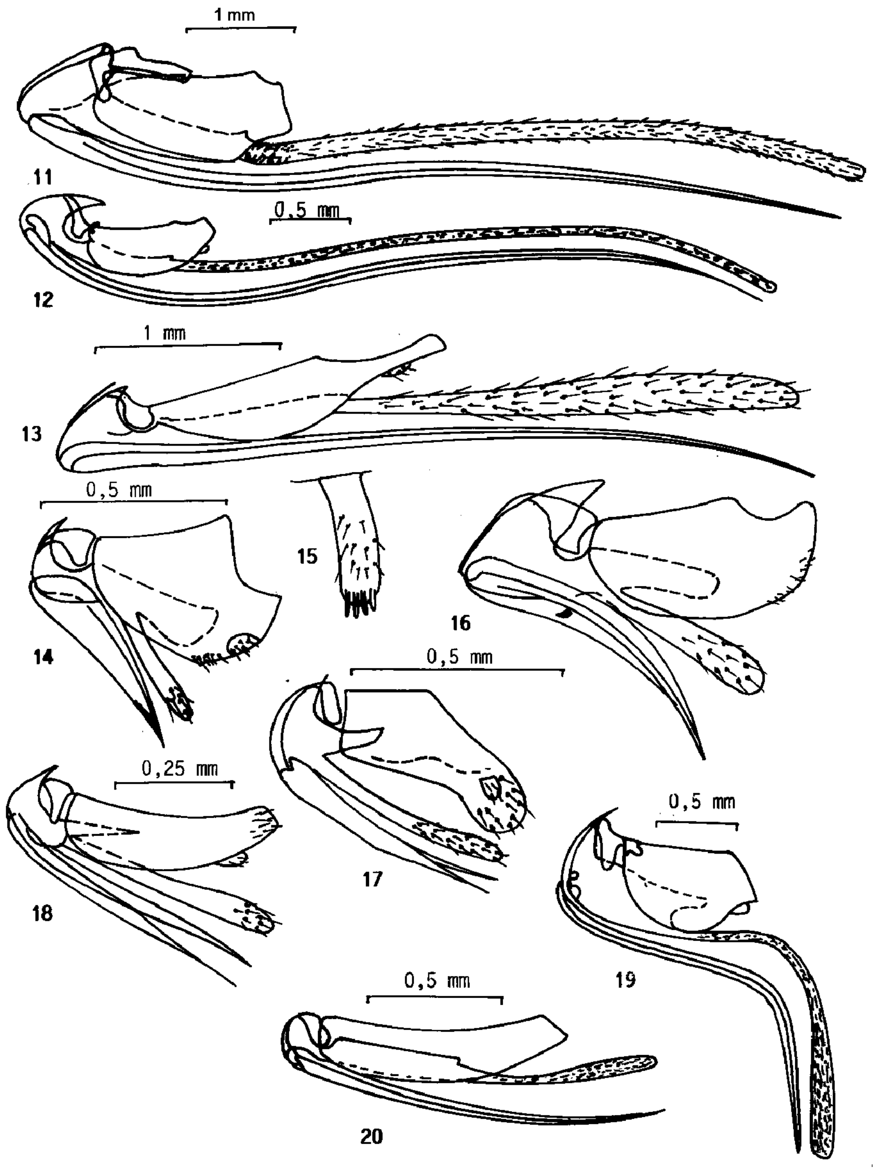
Egg-larval parasitism in a real sense occurs within the subfamily Cheloninae which in many characters is close to microgasterines (Pierce & Holldway, 1912; Bradly, 1941; Caltagirone *et al*, 1964; Rechaw, 1978; Jakson *et al.*, 1978). Adults of this subfamily are easy to recognize since they have a well-developed abdominal carapax built by fusion of the first three tergites. Formation of carapax (Tobias & Dudarenko, 1974) and adaptation to egg-larval parasitism brought about essential changes in the ovipositor structure (Fig. 17). Genital plates are desclerotized. Triangular plates are narrow, oblong ones are very shortened, while the square plates are broken. Valves I and II are wide in the base, but pointed at the tips. When in function they represent micropipets for laying the eggs in host eggs. Valves III are attached to the fore bases of oblong plates and have sensillae on the apexes. Such an ovipositor structure together with the abdomen enables locating the host eggs and successful egg laying. The egg laying itself is not strenuous. It should be noted that the parasite develops simultaneously with the host larva, thus designating the Cheloninae as egg-larval parasites.

The genus *Adelius* which belongs to the subfamily Adeliinae has a very similar ovipositor to that in chelonines (Fig. 18). The species of this genus parasitize caterpillars, minings from the genera *Nepticula* and *Lithocolletis*. Caterpillars of these butterflies are tiny and tender. They live buried in leaves and are weakly mobile, so that parasites'adaptations to egg laying in them produced needle-like forms of valves I and II, reduction of oblong plates and moving of valves III foreward.

A quite specific group in morphology and biology represents Brachistinae (Calyptinae) with its genera *Eubazus*, *Aliolus*, *Triasspis*, *Foersteria*, *Polydegmon* and *Schizoprymnus*. Adults are characterized by more or less developed carapax which is made up of fused abdominal tergites. They parasitize concealed larvae of Coleoptera in which they lay eggs pushing valves I and II into the canals where hosts live. *Triaspis pallidipes* Nees parasitizes larvae of *Rhychaenus fagy* L. which live in leaves and make galles (BEIRNE, 1946). The ovipositor of all the species of brachistines has the same pattern of structure (Fig. 19). Valves are a few times longer than the complex of genital plates. Denticulations on valves I are weakly developed.

A very similar genus to ectoparasitic braconids in its ovipositor structure is the genus *Termitobracon* with the species *T. emersoni* which was found in termite nests, but its biology is unknown. The complex of genital plates of the ovipositor of this species is elongated and valves I have about ten tiny teeth (Fig. 20). This species appears to be an endoparasite of termites.

Alysinae and Opiinae represent two very specialized groups of braconids which parasitize only larvae of Diptera, but there is an egg-larval parasitism within them which appears to be here in the very beginning. Adults of these subfamilies differ considerably. Namely, the Alysinae are the group of braconids in which mandibles are turned outwards and their only function is to cut puparium of the host when an adult emerges (WHARTON, 1984). The majority of species of the family Opiinae in most cases have a broadly emarginate clypeus as ectoparasitic braconids do. Only Exodontiellini have mandibules as those in Alysiinae (WHARTON, 1977). With regard to the fact that larvae of Diptera develop in various substrates, the ovipositor in Opiinae and Alysiins changes considerably making it difficult to give the general pattern of structure for these subfamilies. The most primitively built ovipositors are long with elongated complex of genital plates (Figs. 21, 24), the most advanced ones being short (Figs. 22). The ovipositor of the species belonging to the subfamily Opiinae is more primitive in structure (Fig. 21). It appears that this group is phylogenetically old-



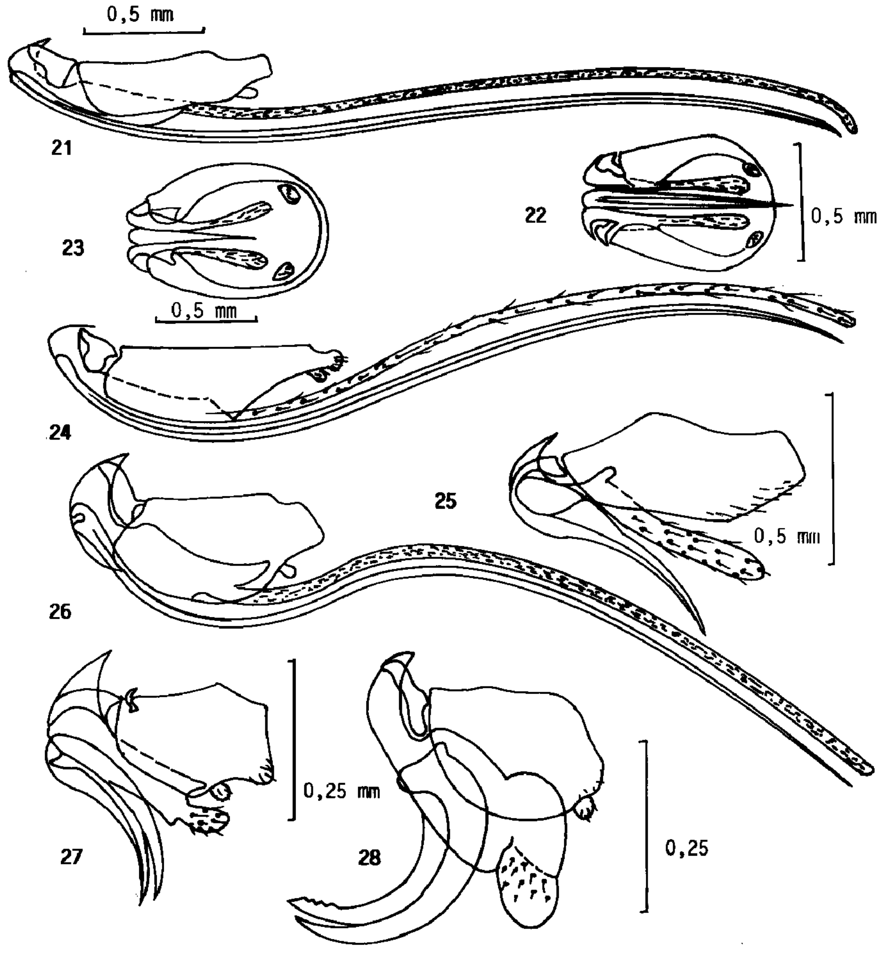
Figs. 11-20; 11. *Agathis perforator* Prov. (Agatjhidinae), 12. *Orgilus medicaginis* Mues. (Orgilinae), 13. *Apanteles crassicornis* Prov. (Microgasterinae), 14. C*otesia congregatus* (Say) (Microgasterinae), 15. *Diolcogaster facetosa* (Wleed) (tip of the third valvae) (Microgasterinae), 16. *Cardiochiles nigriceps* Vier. (Cardiochnlinae), 17. P*hanerotoma fasciata* Prov. (Cheloninae), 18. *Adelius fasciipennis* Rohw. (Adelinae), 19. *Eubazus rotundiceps* (Cress.) (Brachistinae), 20. *Termitobracon emersoni* Brues (Ypsisoocerinae).

er. The complex of genital plates is elongated and in most species the valves I have a few teeth. The valves III are attached to distal parts of oblong plates in all of them. Fewer number of species have a short ovipositor characterized by short and wide plates and short needle-like valves I and II (Fig. 23). Within the subfamily Alysiinae both types of the ovipositor may be encountered, but there is a very pronounced tendency of desclerotization and shortening of plates and valves, while valves I and II receive a needle-like form, whereas valves III move forward as in helinines.

Species of the small subfamily Ichneutinae parasitizing larvae of Symphita also belong to the group of egg-larval parasites. The ovipositor of these species (Fig. 25) has a similar pattern of structure with the ovipositor of some species belonging to the subfamily Cheloninae. It is characterized by short oblong plates to the bases of which wide valves III are attached. Valves I and II are wide at the base but needle-like at the top.

The subfamily Euphorinae represents a very complex group in every respect. Most species of this subfamily parasitize adults of Coleoptera, some parasitize Hymenoptera, while some parasitize Hemiptera and Neuroptera. The species of the genus *Meteorus* parasitize the caterpillars and some larvae of the Coleoptera (CUSHMAN, 1913; JACKSON, 1928; WOLLOFF, 1961, 1967; LOAN, 1964, 1965; LOAN & HOLDWAY, 1961; LOAN *et al* 1969). This is the only group in which adult parasitism developed which brought about essential changes in structure of abdomen and behaviour of females at oviposition. A remarkable trait of the species belonging to the subfamily Euphorinae is petiolate abdomen and a long ovipositor in some species (Fig. 26) and a short one in other (Figs 27, 28). Euphorinae with the long ovipositor at ovipoistion bend the abdomen below the chest and head and pierce the host quickly and precisely with the ovipositor in the regions between segments where sclerotisation is weak. The behaviour of female euphorines at oviposition is very complex; it is well-known, for example, that females of *Dinocampus coccinelae* in order to lay the eggs into the body of adult lady bug, hit them by the ovipositor to induce them to move or lift the wings and thus uncover soft parts of the abdomen. Euphorinae with a short ovipositor also parasitize the adults of Coleoptera and nymphs and adults of Hemiptera. According to some authors this kind of ovipositor is effective since at laying eggs the tip of the ovipositor is at rignt angle in relation to the body of the host so that the piercing itself is more effective. It appears that curved ovipositors, i.e. valves I and II are effective means for piercing ventral part of adult abdomen. A specific and unique is the ovipositor of the genus *Allurus* (Fig. 28) which is short, valves I and II are curved and massive, while valves III are articulated, very sclerotized at the tip and bent forwards. It is well-known that the species of the genus *Allurus* parasitize the adults of *Sitona*. It seems that valves III serve to lift elitre in order to pierce uncovered abdomen by valves I and II. A similar ovipositor is met in the species of the genus *Syrrchizus* which also parasitize adults of hymenopteres.

The subfamily Aphidiinae is very close to the subfamily Euphorinae (Sharkey & Wahl, 1992). The Aphidiinae specialized to parasitize aphids



Figs. 21-28; 21. *Biosteres persulcatus* Silv. (Opiinae), 22. *Biosteres foveolatus* Ashm. (ventral view) (Opiinae), 23. *Chorebusus minuta* Tei. (vemtral view) (Alysiinae), 24. *Pjanerotoma anastrephae* Mues. (Alysiinae), *25. Idchneutes piconematis* Mason (Ichneutinae), 26. *Meteorus versicolor* (Wesm.) (Euphorinae), 27. *Leiophron uniformis* Gah. (Euphorinae), 28. *Allurus lituratns* (Hal.) (Euphorinae).

(Stary, 1970). Most frequently they attack larvae of the second and third stages and some older stages, but rarely adults. At oviposition they are similar to euphorines since their females either curve abdomen and pierce the host from a distance (Hagvar & Hofsvang, 1991), or stand on the host, while the species of the genus *Trioxys* by the tip of abdomen hold the host while laying eggs. Due to this kind of oviposition a very mobile attachment between the second and third abdominal tergites fused on the one side and fourth on the other side has been formed. The ovipositor of aphidiides is very short with curved valves I and II. Valves III are movably articulated with oblong plates and serve as sense organs (Stary, 1976).

The subfamily Hybrizontinae encompasses only the genus *Hybrizon* with two species in Palearctic. The ovipositor of the species *Hybrizon bucata* (Fig. 2) is characterized by short valves I and II which are needle-like at the tip. Valves III are moved forward. According to these traits this species is similar to egg-larval braconids and it may be assumed with great certainty that *Hybrizon bucata* parasitizes eggs and larvae of ants.

CONCLUSION

During evolution of the family and adaptations to parasitizing different groups within the family Braconidae significant changes occurred in the structure of abdomen and ovipositor. For most of them their common trait is that tergites of the second and third segments fuse, and in many species the third one is also fused to them making carapax with a multifold function of protection, stability of the ovipositor, etc. With the development of egg-larval parasitism essential changes of structure occurred in the valves. Valves I and II gained pointed form, valves III widened and lost the function of support retaining the function of sense organs. The ovipositor of the most primitive ectoparasite braconids serves to drill the substrate in which the host lives. That'is why valves I and II have many teeth. During adaptation to parasitising uncovered host, the ovipositor shortens while teeth on the tips of valves I and II become reduced. Endoparasitic braconids specialize to parasitize certain host and consequently the ovipositor changes into several directions. With the development of adult parasitism the ovipositor changes into the organ which in some species functions as bow and arrow, the oviposition being performed from a distance. In other adult parasites the ovipositor gets shorter and valves curve.

Knowledge of changes and tendencies in braconid ovipositor changing is of immense importance. Biology of many species and higher taxa within this group is unknown. Therefore, on the basis of the ovipositor structure it is possible to suppose which hosts are parasitized by a given group. Ovipositor features may be used as significant characters for defining phylogenetic relationships within the family, and in addition to other morphological features for establishing the taxonomy of this great and difficult group from the taxonomical point of view.

ACKNOWLEDGEMENTS

We extend our thanks to the Ministry for Sciences and Technology of Serbia for financial support (Grant application No. 03E04).

REFERENCES

Achterberg, C. van, 1976. A preliminary key to the subfamilies of the Braconidae (Hymenoptera). *Tijdschr. Ent.*, 119, 3: 33-78.

Achterberg, C. van, 1984. Essay on the phylogeny of Braconidae (Hymenoptera, Ichneumonoidea). *Tijdschr. Ent.*, 105: 41-58.

Achterberg, C. van, 1993. Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). *Zool. Verh.*, 283, 189pp.

Allen, W.W., 1958. The biology of *Apanteles medicaginis* Muesembeck (Hymenoptera, Braconidae). *J. Agric. Sc.*, Vol. 27, No. 18: 515-541.

Baht, S. & V.K. Gupta, 1977. Ichneumonologia Orientalis part VI, The subfamily Agathidinae (Hymenoptera, Braconidae), *Oriental Insects Monograph* No.6, Delhi: 1-345.

Beirne, B.P., 1946. Notes on the biology of some hymenopterous parasites of the beech weevil (*Rhynchaenus fagi* L.) (Coleoptera). *Proc. R. Ent. Soc. Lond.* (A) 21. Pts. 1-3: 7-11.

Bradley, W.G., 1941. Methods of breeding *Chelonus annulipes* on the Mediterannean flour moth for use against the European corn borer. *Circular No. 616, U.S.D.A*: 1-23.

Caltagirone, L.E., K.P. Shea & G.L. Finney, 1964. Parasites to aid control of novel orangeworm. *California Agriculture*, 18 (1):10-12.

Cardona, C. & R.E. Oatman, 1971. Biology of *Apanteles dignus* (Hymenoptera, Braconidae) a primary parasite of the tomato pinworm. *Ann. Ent. Soc. Am.*, Vol. 64, No. 5: 996-1007.

Cushman, R.A., 1913. Biological notes on a few rare or little known parasitic Hymenoptera. *Proc. Ent. Soc. Wash.* Vol. XV, No.4: 153-160.

Fink, D.E., 1926. The biology of *Macrocentrus ancylivora* Rohwer an important parasite of the strawberry leaf roller (*Ancylis comptana* Froehl.). *J. Agric. Res.*, Vol. XXXII, No. 2: 1121-1134.

Haeussler, G.J., 1932. *Macrocentrus ancylivorus* Roh. an important parasite of the oriental fruit moth. *J. Agric. Res.*, Vol. 45, No. 2: 79-100.

Hafez, M., 1951. Notes on the introduction and biology of *Microplitis demolitor* Wilk., *Bull. Soc. Fouad. Ent.*, XXXV: 107-121.

Hagvar, B.E. & T. Hofsvang, 1991. Aphid parasitoids (Hymenoptera, Aphidiidae): biology, host selection and use in biological control. *Biocontrol News and Information*, vol. 12, No.1, 13-41.

Jackson, C.G., J.S. Delph & E.G. Heemann, 1978. Developmental longevity and fecundity of *Chelonus blackburni* (Hymenoptera, Braconidae) as a parasite of *Pectinophora gossipiella* (Lepidoptera, Gelechiidae). *Entomophaga*, 23 (1): 35-42.

Jackson, D.J., 1928. The biology of *Dinocampus* (*Perilitus*) *rutilus* Nees, a braconid parasite of *Sitona lineata* L.. Part I, *Proc. Zool. Soc. part.* 2: 597-630.

Loan, C.C., 1964. The bionomics of *Sitona seissifrons* (Coleoptera, Curculionidae) and its parasite *Microctonus sitone* (Hymenoptera, Braconidae). *Ann. Ent. Soc. Am.*, Vol. 56: 600-612.

Loan, C.C., 1965. Life cycle and development of *Leiophron pallipes* Curtis (Hymenoptera: Braconidae, Euphorinae) in five Mirid host in the Belleville district. *Proc. Ent. Soc. Ontario*, 95: 115-121.

Loan, C.C. & F.G. Holdaway, 1961. *Microctonus aetiops* (Nees) and *Perilitus rutilus* (Nees) (Hymenoptera, Braconidae), european parasites of *Sitona weevils* (Coleoptera, Curculionidae). *Can. Ent.*, vol. XCIII, No. 12: 1057-1079.

Loan, C.C. , M.G. Klein & H.C. Coppel, 1969. *Microctonus glyphosceli* n.sp., a parasite of *Glyptoscelis pubescens* (E) in Wisconsin. *Proc. Ent. Soc. Wash.*, Vol. 71, No. 2: 230-233.

Marsh, P., 1965. The Nearctic Doryctinae I. A review of the subfamily with taxonomic revision of the tribe Hecabolini (Hymenoptera, Braconidae). *Ann. Ent. Soc. Am.*, Vol. 58, No. 5: 668-699.

Marsh, P., 1979. Family Braconidae pp. 144-295. In Krombein, K.V. et al., *Catalog of Hymenoptera in America North of Mexico*, Vol. I. Smiths. Inst. Press, Washington, D.C.

Marsh, P., 1991. Description of a phytophagous doryctine braconid from Brazil (Hymenoptera, Brconidae). *Proc. Ent. Soc. Wash.*, 93, 92-95.

Marsh, P.M., S.R. Shaw & R.A. Wharton, 1987. An identification manual for the North American genera of the family Braconidae (Hymenoptera). *Mem. Ent. Soc. Wash.*, Number 13, 98 pp..

Matthews, R.W., 1974. Biology of Braconidae. *Ann. Rev. Ent.*, Vol. 19: 15-32.

Muesebeck, C.F.W., 1937. A new West Indian species of *Mirax* Haliday parasitic on the coffee leaf-miner (Hymenoptera: Braconidae). *Proc. Ent. Soc. Wash.*, 39: 139-141.

Papp, J., 1974. A study on the systematics of Braconidae (Hymenoptera). *Folia Ent. Hung.* (Ser., nova) XXVII, 2: 109-133.

Parker, H.L., 1931. *Macrocentrus gifuensis* Ashm., a polyembrionic braconid parasite in the European corn borer. *Tech. Bull.*, No. 230: 1-62.

Pierce, W.D. & T.E. Holldway, 1912. Notes on the biology of *Chelonus texanus* Cress.. *J. Econ. Ent.*, Vol. 5, No. 6: 425-428.

Rechav, Y., 1978. Biological and ecological studies of the parasitoid *Chelonus inanitus* (Hymenoptera: Braconidae) in Israel. *Entomophaga*, 23 (I): 95-102.

Stary, P., 1970. Biology of aphid parasites (Hymenoptera, Aphidiidae) with respect to integrated control. *Ser. ent.* 6: 643 pp. W. Junk, The Hague.

Stary, P., 1976. External female genitalia of the Aphidiidae (Hymenoptera). Acta *Entomologica Bohemoslovaca*, 73: 102-112.

Stultz, H.T., 1954. Note on occurrence of *Agathis laticinctus* (Cress.) (Hymenoptera: Braconidae) as a parasite of the Eye-Spotted Bud Moth (Lepidoptera: Tortricidae) in Nova Scotia. *Can. Ent.*, Vol. LXXXVI, No.2: 96-98.

Sharkey, M.J. & D.B. Wahl, 1992. Cladistics of the Ichneumonoidea (Hymenoptera). *J. Hym. Res.*, 1 (1), 15-24.

Tadić, M.D., 1959. *Apanteles hyphantriae* Riley, an egg parasite of the fall webworm. *Proc. 10th Int. Cong. Ent.*, Montreal, 4: 859-861.

Tobias, V.I, 1967. A review of the classification, phylogeny and evolution of the family Braconidae (Hymenoptera). *Ent. Obozr.*, 46, 645-669 (in Russian).

Tobias, V.I., and Dudarenko, G.P. 1974. General trends in evolution of Braconidae (Hymenoptera) abdomen. *Vest. Zool.*, 1974 (3):65-72. (In Russian).

Tobias, V.I, Belokobilskij, S.A, Kotenko, A.G 1986. *Key to Insects of the European part of U.S.S.R T.III: Hymenoptera.* IV part, 509c. (In Russian).

Vance, A.M., 1932. The biology and morphology of the braconid *Chelonus annulipes* Wesm., a parasite of the European Corn Borer. *Tech. Bull.*, No. 294: 1-48.

Waloff, B.N., 1961. Observation on the biology of *Perilitus dubius* (Wesmael) (Hymenoptera, Braconidae), a parasite of the Chrysomelid beetle *Phytodecta olivacea* (F–rster). *Proc. R. Ent. Soc. Lond.*, (A) 36, pts. 7-9: 96-102.

Waloff, B.N., 1967. Biology of the three species of *Leiophron* (Hymenoptera, Braconidae, Euphorinae) parasitic on Miridae on Brom. *Trans. R. Ent. Soc. Lon.*, 118, (6): 187-213.

Wharton, R.A., 1984. *Biology of the Alysiini (Hymenoptera, Braconidae), parasitoids of cyclorrhaphous Diptera.* Dept. of Ent. Tex. Agric. Exp. St. and Tex. A & M Univ., Tec., monograph 11: 1-39.

WILBERT, H., 1960. *Apanteles pieridis* (Bouche) (Hymenoptera, Braconidae), ein parasit von *Aporia crataegi* (L.) (Lepidoptera, Pieridae). *Entomophaga*, 5: 183-211.

ZLATANOVA, A.A., 1970. Biology of the *Microdus rufipes* Nees (Hymenoptera, Braconidae) parazitoid jablonoy plodorosky in Kazachstan. *Ent. Obozr.* XLIX, 4: 749-755. (In Russian).

МОРФОЛОШКЕ АДАПТАЦИЈЕ ОВИПОЗИТОРА БРАКОНИДА (BRACONIDAE: HYMENOPTERA) ВЕЗАНЕ ЗА БИОЛОШКЕ КАРАКТЕРИСТИКЕ ЊИХОВИХ ДОМАЋИНА

М. БРАЈКОВИЋ, М. КРУНИЋ, Ж. ТОМАНОВИЋ И Љ. СТАНИСАВЉЕВИЋ

Извод

Током дуготрајне еволуције браконида развиле су се две групе: ектопаразитске и ендопаразитске. Ектопаразитизам је у оквиру групе по многима раније настао у филогенији браконида. Ектопаразитске браконидe су мање обимне и мање специјализоване. Паразитирају ларве Coleoptera, Lepidoptera, Hymenoptera и Diptera. Оне при полагању јаја буше супстрат у којем живи домаћин и трајно парализу ларву домаћина. Код већине је у вези са овим легалица дуга, а валве I и II су на врховима назубљене. У оквиру ектопаразитских браконида је врло изражен тренд скраћивања легалице и редукције зубића на валвама I и II јер се прилагођавају на паразитирање мање заштићених или откривених ларви.

Ендопаразитске браконидe су знатно обимније. Имају шири спектар домаћина и поред развојних ступњева Coleoptera, Lepidoptera, Hymenoptera, Diptera оне паразитирају врсте из редова Hemiptera, Heteroptera, Mecoptera и вероватно још неких јер је биологија већине непозната. У оквиру ендопаразитских браконида се поред ларвалног као доминантног облика паразитизма јављају још јајно-ларвални и имагинални паразитизам. Са развојем јајно-ларвалног паразитизма одвијају се битне

промене у грађи валви, при чему се валве I и II скраћују, добијају игличасту форму на врховима и зубићи се потпуно редукују. Валве III се проширују и губе функцију потпоре, а задржавају само функцију чулних органа. Развојем имагиналног паразитизма легалица је дуга и служи за убадање имага домаћина са извесне дистанце чиме се женка паразита штити од евентуалног напада домаћина. Код неких имагиналних паразита, легалица се пак скраћује, валве се лучно савијају и служе за више функција, узнемиравање имага домаћина, подизање елитри и убадање домаћина, а сам акт полагања јаја се врши са тела домаћина. У оквиру ендопаразитских браконида битне промене у грађи легалице се одвијају и у зависности од места где се развијају ларве домаћина. Промене се одвијају у грађи гениталних плоча, а још више у грађи валви.

Познавање промена и тенденција промена у грађи легалице браконида има вишеструки значај. Билогија огромног броја врста у оквиру групе се уопште не зна, па на основу грађе легалице могуће је бар претпоставити које домаћине паразитирају. За ову сврху рад на упоредноморфолошким истраживањима грађе легалице браконида треба наставити и проширити на што је већи број таксона јер је недавно описано неколико подфамилија.

Received December 28, 1999
Accepted March 27, 2000