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MALE GENITALIA OF THE SPECIES OF THE SUBFAMILY AGATHIDINAE (HYMENOPTERA: BRACONIDAE) AND THEIR IMPORTANCE IN TAXONOMY

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Abstract – A morphological analysis of the male genitalia of 24 species of the subfamily Agathidinae from 10 genera is presented. Detailed descriptions of important morphological features of all the species are given. Their value in the identification of the species was assessed. It was found that the morphology of male genitalia could be used for identification of the genera, while it was of limited value at the species level, except for those belonging to multispecific genera.

Key words: Braconidae, Agathidinae, male genitalia, morphology

UDC 595.79.06

INTRODUCTION

Agathidinae are solitary koinobiont endoparasitoids of lepidopteran larvae. Most of the species described are from tropical and subtropical regions, but some are from temperate areas. Imagoes of this subfamily are characterized by elongated labio-maxillary complex and elongated genae, which make them easy to recognize. In addition, they have a short radial cell and a small second cubital cell on their wings. Their first instar larvae have projections on the thoracic and abdominal segments, which presumably have function in locomotion.

The systematics of Agathidinae is quite questionable and is based primarily on the morphological characteristics of the head, wing venation, and others (Telenga, 1955; Tobias, 1976, 1986). Nixon (1986) revised European Agathidinae and established 54 valid species and 11 synonyms. The tropical fauna of Agathidinae is richer, but less studied. It was investigated by Bacht and Gupta (1977) and Chou and Sharkey (1989). Recently, Simbolotti and Achterberg (1999) revised the West Palaearctic species of the genus *Agathis* Latreille and provided a detailed key for the identification of the Palaearctic species. They used the meristic characteristics of the head (form of the clypeus and malar triangle, shape of the frons, occiput, and face) and fore wings for identification of the species. Special attention was paid to the ratios between nerves 1-R1 and 1R1 of the fore wings and the length of the pterostigma. The diagnostic value of the following characteristics is questionable because they are mostly unstable: color, length of body, length of mouthparts, etc. In all the papers which deal with the taxonomy of Agathidinae difficulties in the identification of genera and species are mentioned because this group is extremely variable. In the old studies on this group different attention was paid to distinctive characters, primarily to the shape of the mouthparts, propodeum, and pleurae, length of valvae of the ovipositor (ovipositor sheaths), and characteristics of the wing venation. According to Simbolotti and Achterberg (1999), all these structures (except the mouthparts) are variable, which Tobias (1963) and Nixon (1986) have also shown.

The male genitalia of insects are very specific in form in higher taxa (orders and families), but quite uniform at generic and specific levels (Matsuda, 1976). In various groups of insects their high stability was

observed, making male genitalia in some groups the main criterion for identification of the species. The male genitalia are also the basis for establishing the origin and evolution of these structures (Snodgrass, 1941; Michener, 1944; Gustafson, 1950; Nielsen, 1957). As for the origin of these structures, Matsuda (1976) showed that they differentiated from the lobe at the end of IX or between IX and X abdominal segments. It was found that the primary phallus lobes in Hymenoptera formed at the end of IX abdominal segment (D'Rozario, 1942).

The male genitalia of Braconidae have been investigated sporadically (Soliman, 1941; Alam, 1952; Telenga, 1952; Tobias, 1963, 1976, 1986; Marsh, 1965; Belokobiljskij, 1987; Brajković, 1989; Maeto, 1996). From the above-mentioned papers it may be concluded that the copulatory parts of braconids have a unique pattern and consist of a basal ring (lamina annularis), paramerae (lamina parameralis), volsellae with cuspis and digitus, and aedeagus.

The basal ring varies both in form and size. In more primitive groups it is massive, conical, and closed basally in dorsal view. According to Tobias (1963, 1976), the general trend in the evolution of this part is its reduction, i.e., shortening to complete disappearance (Brajković, 1989). Paramerae are laterally tubular plates, which extend from the basal ring and surround all other structures. The bases of paramerae are commonly named basiparamerae, while their distal parts are paramerae. Such designation is unnecessary in Braconidae because these parts are not separated, but make up one unit. Setae exist at the apex of paramerae in all the Braconidae investigated to date. The shape, size, number and type of parameral setae vary considerably within all levels of taxa. Volsellae are median plates, which basally may possess pointed lateral projections forming apodemae volsellaris. On the distal part of the volsellae cuspides are placed, while digiti are medially placed. The degree of cuspis development varies in Braconidae. Digiti represent unarticulated parts of the volsellae. They vary very much in the form, size, and number of teeth on the outer margins, but are of specific form in each of the species. Therefore, they have the greatest diagnostic value. The aedeagus comprises paired valvae furnished with apodemae and pointed ergots, and are distally conical. The morphology of aedeagus valvae is different in different taxa.

MATERIAL AND METHODS

To investigate the male genitalia of Agathidinae, 24 species belonging to the subfamily with various geographical distributions were chosen. Most of the material originates from the collection of the Systematic Entomology Laboratory, Natural History Museum, Washington D.C., USA, while the remaining part comes from the collection of the Institute of Zoology, Faculty of Biology, University of Belgrade, Belgrade, Serbia. Dissected structures were treated by the standard method of making chitin slides. They were cooked in 10% KOH, rinsed in 65-100% alcohol, and then placed in xylol and mounted on slides in Canada balsam. Terms for male genitalia are taken from Snodgrass (1941).

A list of examined species:

Agathis agilis (Cresson, 1873)

A. calcaratus (Cresson, 1873)

A. erythrogaster Viereck, 1913

A. gibbosus (Say, 1836)

A. fuscipennis (Zetterstedt, 1838)

A. montana Shestakov, 1932

A. nigra Nees, 1812

A. perforator Provancher, 1880

A. simillimus (Cresson, 1873)

A. stigmaterus (Cresson, 1865)

A. texanus (Cresson, 1872)

Megagathis albitarsis (Cresson, 1865)

Agathirsia nigricaudus (Viereck, 1905)

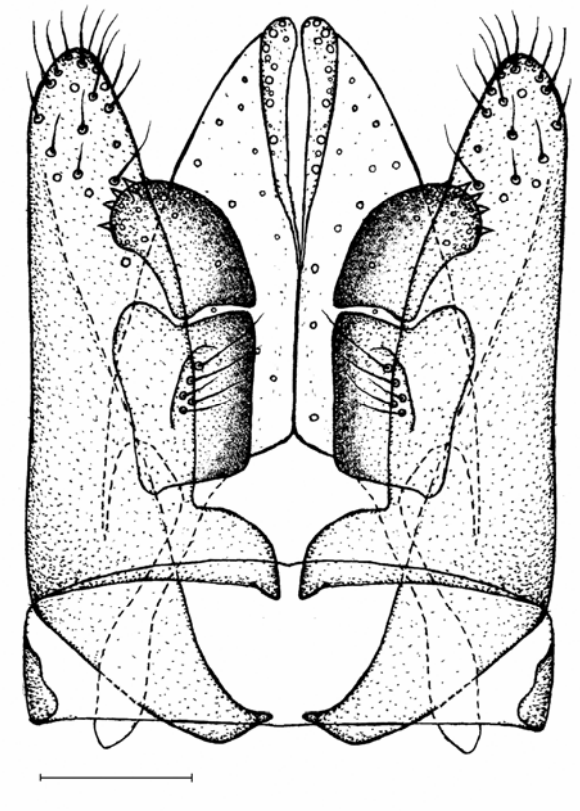

Fig. 1. Male genitalia of *Agathis agilis* (Cresson, 1873). Scale bar 0.1 mm.

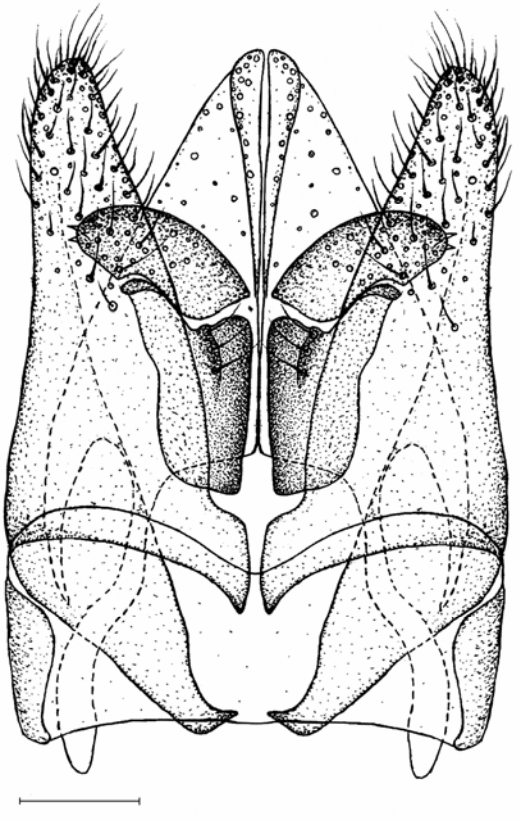

Fig. 2. Male genitalia of *Agathis calcaratus* (Cresson, 1873). Scale bar 0.1 mm.

A. testacea Muesebeck, 1927

Cremnops haematodes (Brulle, 1846)

C. vulgaris (Cresson, 1865)

C. montrealensis (Morrison, 1917)

Bassus festivus (Muesebeck, 1953)

Microdus pumilus Ratzeburg, 1844

Crassomicrodus pallens (Cresson, 1873)

C. medius (Cresson, 1865)

Earinus gloriatorius (Panzer, 1809)

Zelomorpha arizonensis Ashmead, 1900

Disophrys caesia (Klug, 1835)

RESULTS

The species belonging to the genus Agathis (A. agilis, A. calcaratus, A. erythrogaster, A. gibbosus, A. fuscipennis, A. montana, A. nigra, A. perforator, A. simillimus, A. stigmaterus, and A. texanus) (Figs. 1-11) have similar copulatory organs at first glance, but they differ considerably in detail.

The basal ring in all the species is band-like, varying in width. In all the analyzed species it is dorsally opened, with short projections connected by a membrane.

The paramerae of the species belonging to *Agathis* are of the same structure, but their length is different (in relation to the apex of aedeagus valvae). In *Agathis stigmaterus*, *A. gibbosus*, *A. simillimus*, *A. erythrogaster*, and *A. agilis* they do not

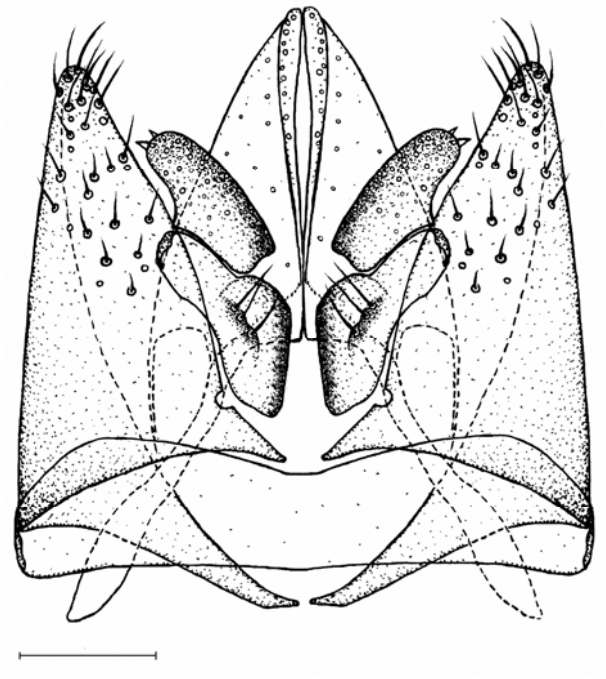

Fig. 3. Male genitalia of *Agathis erythrogaster* Viereck, 1913. Scale bar 0.1 mm.

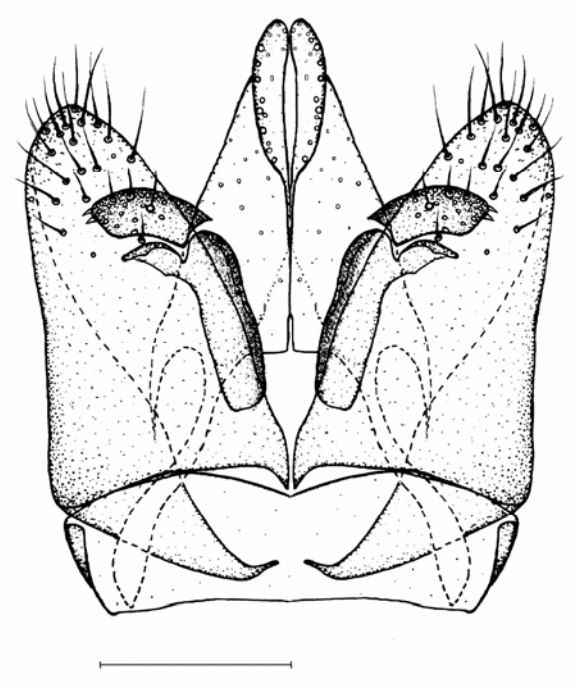

Fig. 4. Male genitalia of *Agathis gibbosus* (Say, 1836). Scale bar 0.1 mm.

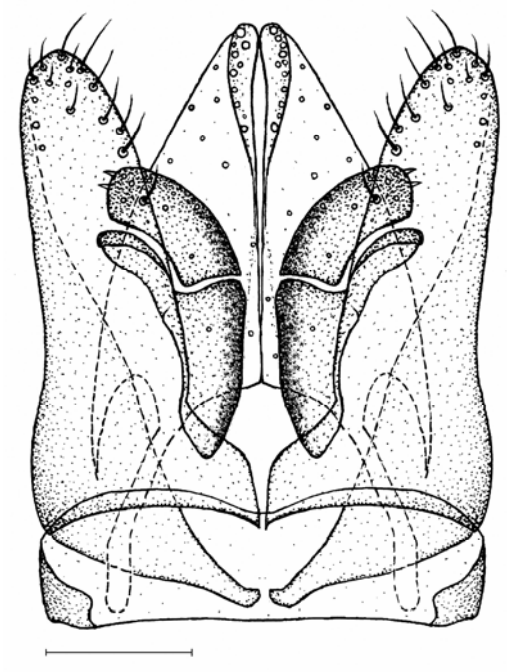

Fig. 5. Male genitalia of *Agathis fuscipennis* (Zetterstedt, 1838). Scale bar 0.1 mm.

exceed the aedeagus valvae apex, while in *Agathis texanus* and *A. calcaratus* they exceed the apex of aedeagus valvae. Both the arrangement and the number of setae are different in the different species. Thus, in *Agathis stigmaterus*, *A. gibbosus*, and *A. simillimus* the setae cover almost the entire paramerae, while in other species they are less abundant and are found only apically.

The volsellae of the studied species are short, wide, and without apodemae. There is a difference in the degree of sclerotization of their distal and inner margins. In *Agathis calcaratus* and *A. perforator* these margins are very sclerotized, whereas in others they are membranous. The volsellae of *Agathis agilis*, *A. calcaratus*, *A. erythrogaster*, *A. simillimus*, *A. stigmaterus*, *A. texanus*, *A. perforator*, and *A. testacea* bear 2-5 setae. In *Agathis gibbosus*, *A. nigra*, and *A. fuscipennis* setae do not exist.

The cuspides of the *Agathis* species differ in their development. In *Agathis stigmaterus*, *A. perforator*, and *A. agilis* they are poorly developed, while

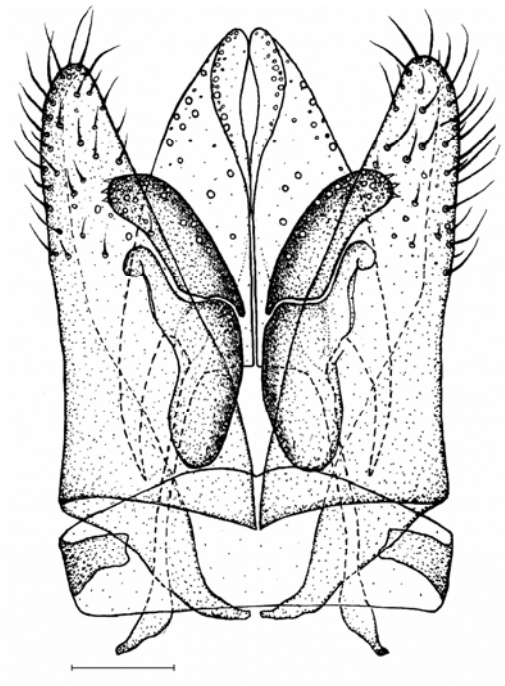

Fig. 6. Male genitalia of *Agathis montana* Shestakov, 1932. Scale bar 0.1 mm.

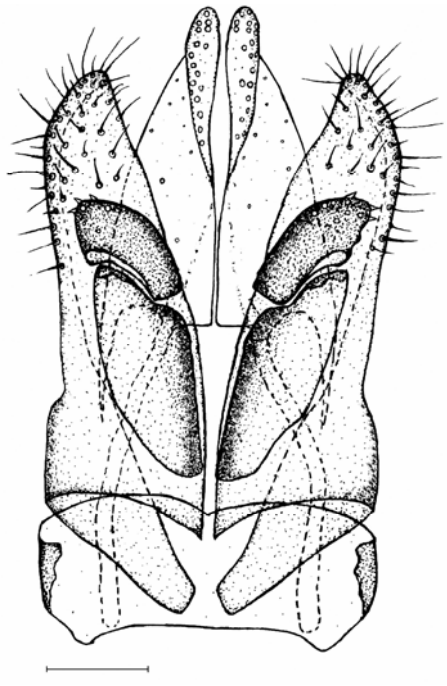

Fig. 7. Male genitalia of *Agathis nigra* Nees, 1812. Scale bar 0.1 mm.

in other species they are larger, extending to the mid-digitus, while in *Agathis texanus* and *A. fuscipennis* they are shorter than the digiti.

Digiti in most of the species are invertely L-shaped, while in *A. agilis* they are rounded. The apices of the digiti have different numbers of teeth, from one to several. The aedeagus of the studied species is characterized by short valvae, which are widened basally, and with very prominent ergots. The valval apodemae are also short and do not exceed the base of the basal ring. Phallotrema in all the species is wide.

The male genitalia of the species *Megagathis albitarsis* (Fig. 12) are characterized by a band-like basal ring which is slightly sclerotized. The paramerae are conical, narrow and mostly covered by scarce setae. The paramerae nearly reach the apex of the aedeagus. The volsellae in this species are very short, without apodemae, and with a very sclerotized anterior margin which is furnished with six setae. The cuspides are small, while the digiti are

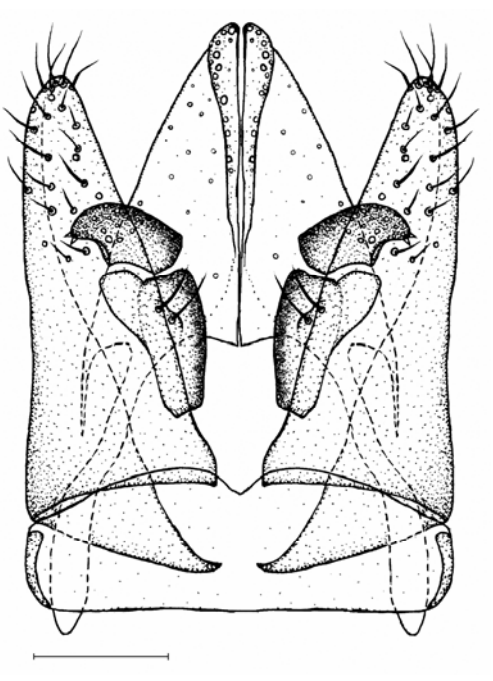

Fig. 8. Male genitalia of *Agathis perforator* Provancher, 1880. Scale bar 0.1 mm.

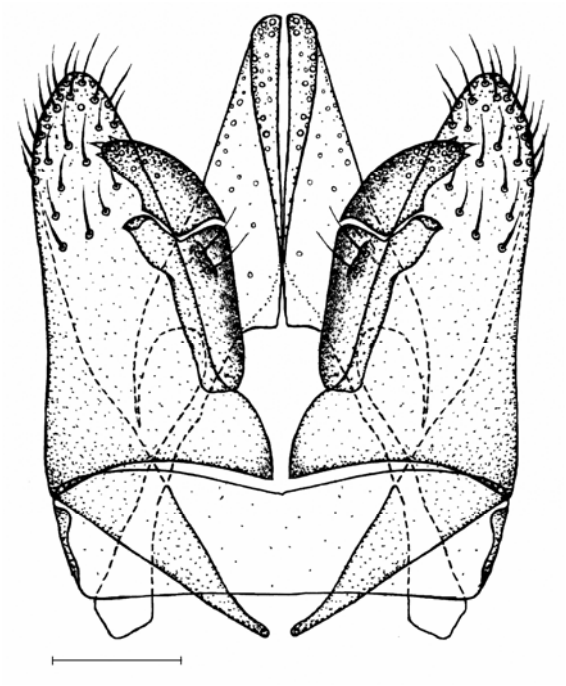

Fig. 9. Male genitalia of *Agathis simillimus* (Cresson, 1873). Scale bar 0.1 mm.

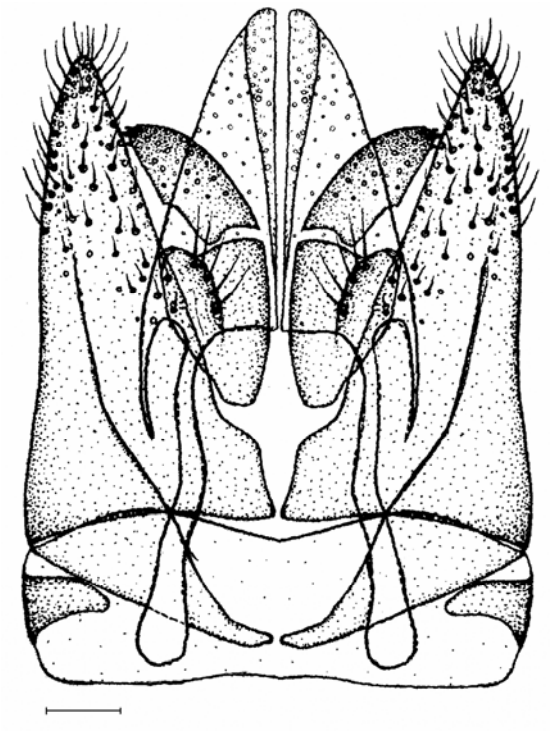

Fig. 10. Male genitalia of *Agathis stigmaterus* (Cresson, 1865). Scale bar 0.1 mm.

large, bent and have more teeth on the entire surface. The valvae of the aedeagus are fairly long and narrow. They have long apodemae basally, exceeding the lumen of the basal ring.

The species of the genus *Agathirsia* Westwood (*A. nigricaudus* and *A. testacea*) have a similar structure of the male genitalia.

The basal ring in both the species is in the form of a dorsally opened band.

The paramerae of *Agathirsia nigricaudus* (Fig. 13) are wide basally, the distal parts are narrow, and the apices exceed the apex of the aedeagus. The basal part of each paramera is covered with sparse setae. The paramerae of *Agathirsia testacea* (Fig. 14) are wide basally and narrow in the remaining part and apically, bearing sparse setae. The apices slightly exceed the aedeagus apex.

The volsellae of *Agathirsia testacea* are wide and short, without apodemae. They are covered with

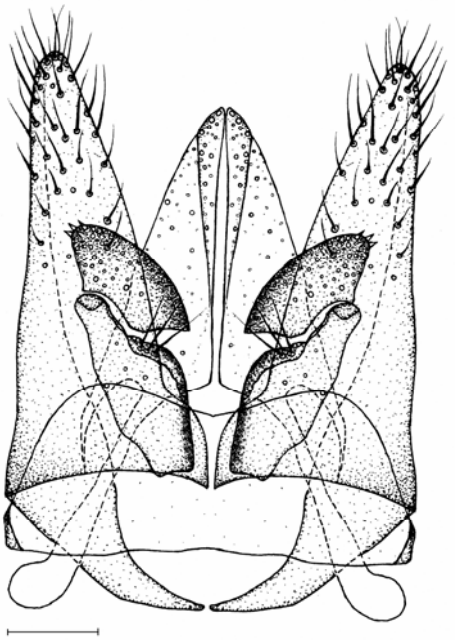

Fig. 11. Male genitalia of *Agathis texanus* (Cresson, 1872). Scale bar 0.1 mm.

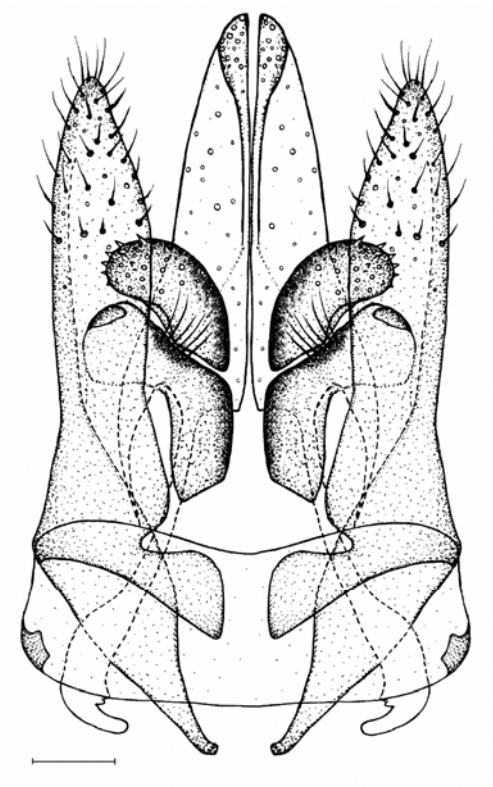

Fig. 12. Male genitalia of *Megagathis albitarsis* (Cresson, 1865). Scale bar 0.1 mm.

five setae. The volsellae of *Agathirsia nigricaudus* are considerably narrower and longer, with four setae.

The cuspides in *Agathirsia nigricaudus* are large, while in *Agathirsia testacea* they are remarkably less developed.

The digiti of *Agathirsia nigricaudus* are fairly elongated, carrying two teeth apically, while in *A. testacea* they are short, carrying three teeth.

The aedeagi in both species are similar in shape, but in *A. nigricaudus* the apodemae of the valvae are longer and distally rounded.

The species belonging to the genus *Cremnops* Foerster, 1862 (*C. haematodes*, *C. vulgaris*, and *C. montrealensis*) (Figs. 15-17) show the greatest similarity in copulatory structures. Their basal ring,

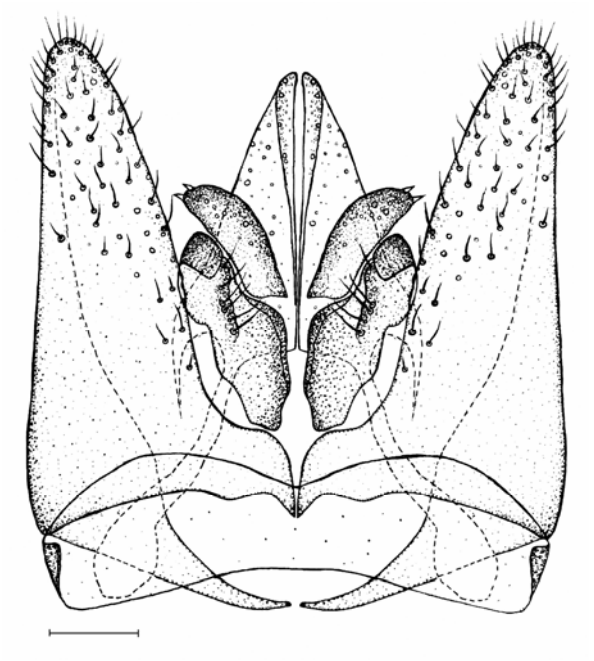

Fig. 13. Male genitalia of *Agathirsia nigricaudus* (Viereck, 1905). Scale bar 0.1 mm.

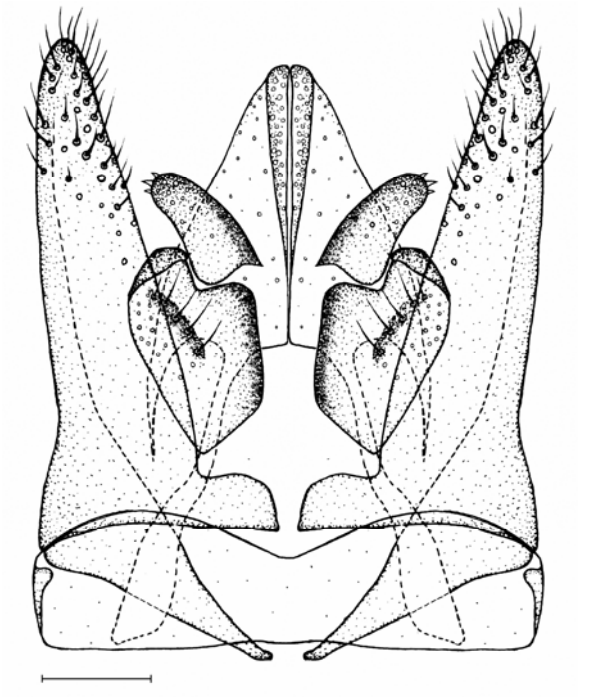

Fig. 14. Male genitalia of *Agathirsia testacea* Muesebeck, 1927. Scale bar 0.1 mm.

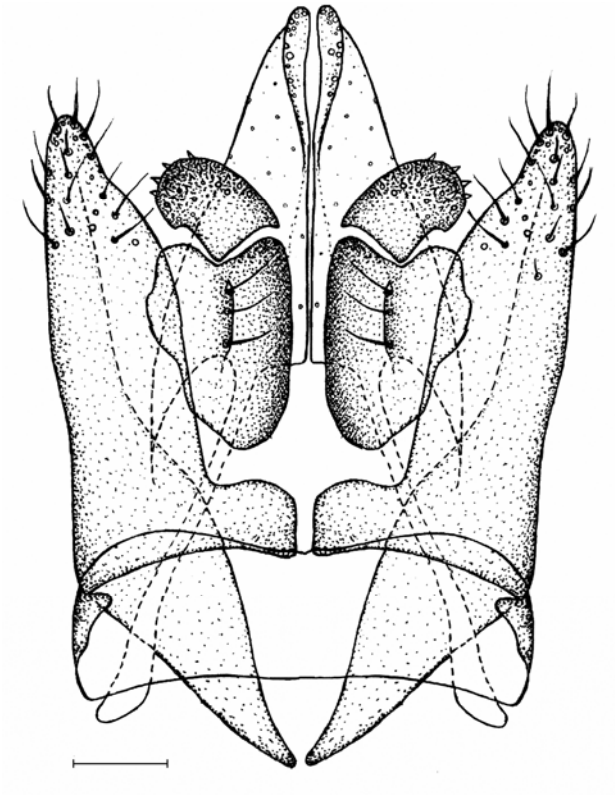

Fig. 15. Male genitalia of *Cremnops haematodes* (Brulle, 1846). Scale bar 0.1 mm.

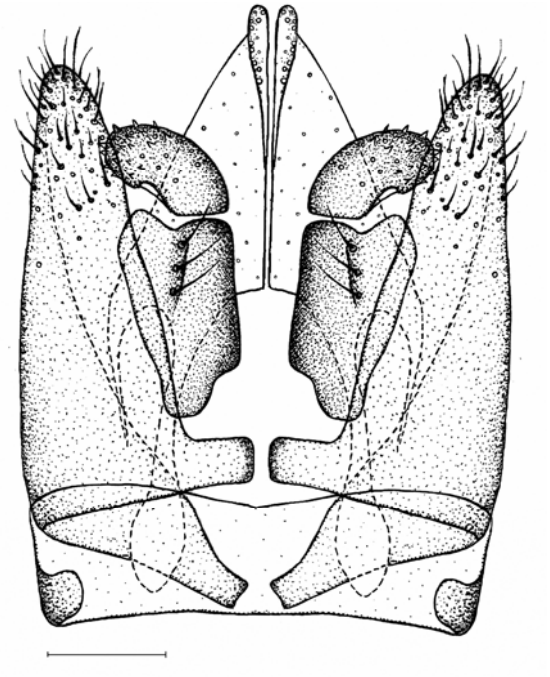

Fig. 16. Male genitalia of *Cremnops vulgaris* (Cresson, 1865). Scale bar 0.1 mm.

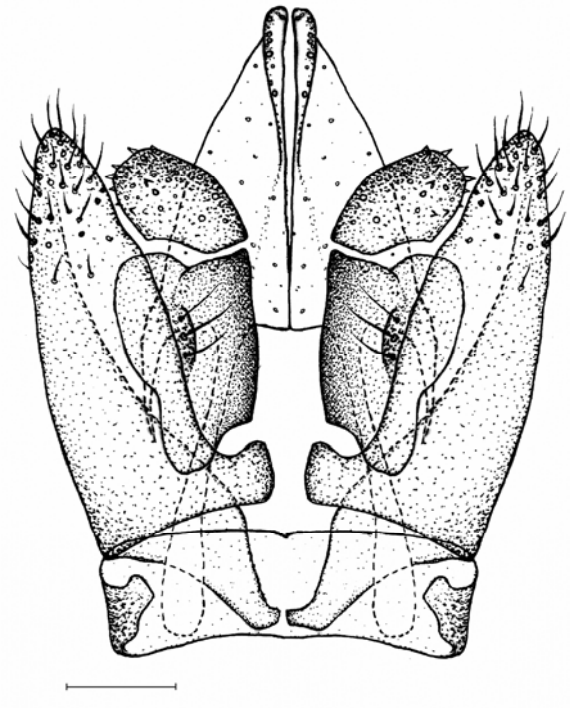

Fig. 17. Male genitalia of *Cremnops montrealensis* (Morrison, 1917). Scale bar 0.1 mm.

in comparison to all other Agathidinae, is more sclerotized, wide, dorsally with short ends connected by a membrane. Differences in length of the basal ring are hardly noticeable. The paramerae are similar, short and wide, bearing sparse setae apically. They do not reach the apex of the aedeagus. The volsellae are short, very wide, with a very sclerotized interior margin. The cuspides are weakly developed, hardly noticeable. The digiti are rounded and massive, with more than 15 teeth.

The aedeagus is with a wide phallotrema. The aedeagus valvae are with large ergots and short apodemae, which only in *Cremnops haematodes* come out from the basal ring.

The copulatory structures of the species *Bassus festivus* (Fig. 18) are in the form of a band, while its paramerae are conical, with few setae at the apex. The volsellae are narrow, with two setae. The cuspi-

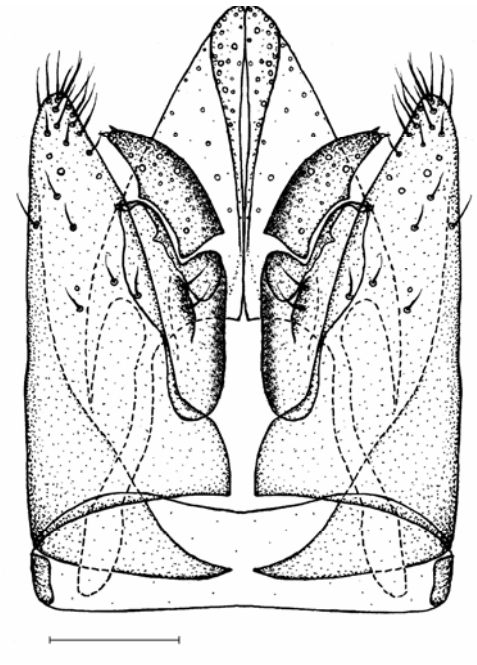

Fig. 18. Male genitalia of *Bassus festivus* (Muesebeck, 1953). Scale bar 0.1 mm.

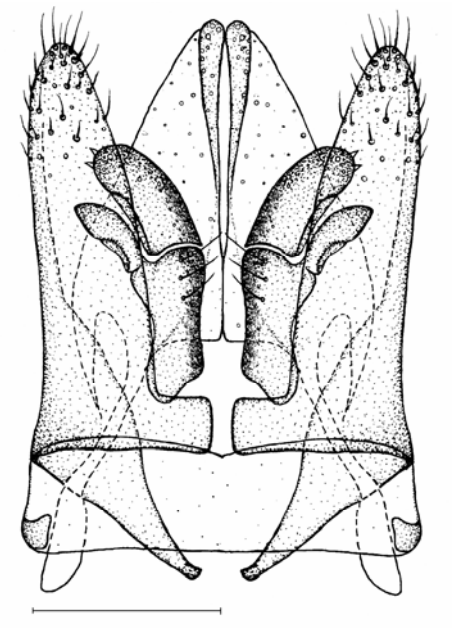

Fig. 19. Male genitalia of *Microdus pumilus* Ratzeburg, 1844. Scale bar 0.1 mm.

des of this species are well-developed, narrow, and reach the mid-digitus. The digiti are slightly bent, pointed, with two teeth. The aedeagus valvae are short, wide, with large ergots, and a wide phallotrema. The aedeagus apodemae do not exceed the lumen of the basal ring.

The copulatory organ of the species *Microdus pumilus* (Fig. 19) is characterized by a band-shaped basal ring. The paramerae are wide only basally, but narrow along the remaining part. Setae occur only at the apices.

The volsellae are narrow, sclerotized along the median margin, with three setae. The cuspides are narrow and elongated. Digiti are massive, rounded at the apex, with two teeth.

The aedeagus valvae are wide, ergots are large, while the apodemae are long, exceeding the lumen of the basal ring.

The species belonging to the genus *Crassomicrodus* Ashmead (*C. pallens* and *C. medius*) (Figs. 20 and 21) each have a band-like basal ring. The dorsal ends are short, connected by a membrane. The paramerae have short, but wide basiparamerae. The distal parts are considerably narrower and furnished with few setae.

The volsellae are short, wide, well-sclerotized interiorly. The cuspides are irregular in form. The digiti are large, bent, in *Crassomicrodus medius* these are long, with more than 15 teeth, while in *C. pallens* with two teeth.

The aedeagi have the same form, with a wide phallotrema in *C. pallens.*

The species *Earinus gloriatorius* (Fig. 22) differs from other Agathidinae species in many of the characteristics of its copulatory organs. The basal ring is very massive, with dorsally pointed long ends. The paramerae are also massive, wide, with a few setae apically. The volsellae are narrow and bent. The digiti are narrow and long, each with a tooth apically.

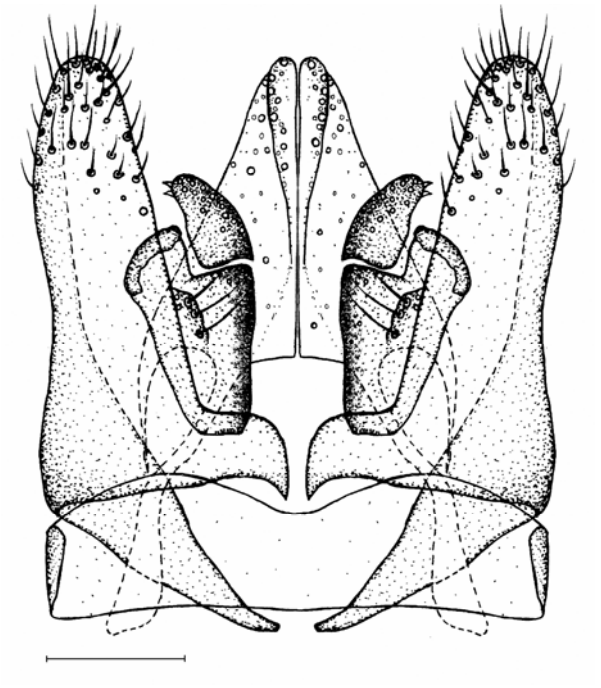

Fig. 20. Male genitalia of *Crassomicrodus pallens* (Cresson, 1873). Scale bar 0.1 mm.

The aedeagus valvae are short, considerably longer than its paramerae. Valval apodemae are the longest in this species.

The copulatory organ of *Zelomorpha arizonensis* (Fig. 23) has a short basal ring. The paramerae are massive, gradually narrowing apically, where sparse setae occur. The volsellae are wide and more sclerotized interiorly. The cuspides are small, of irregular shape. The digiti are massive, with two teeth apically.

The genitalia of *Disophrys caesia* (Fig. 24) are strongly sclerotized. The basal ring in most Agathidinae is in the form of a transverse stripe. Its paramerae are conical and massive. Sensillae occur at ends of the interior sides. The volsellae are narrow, elongated, without a cuspis. The digiti are narrow, bent, with three teeth apically. The valvae of the aedeagus are massive, with eight wide phallotremae. The apodemae are very narrow and long. In general, the genitalia of this species are the closest to those in *Earinus gloriatorius*.

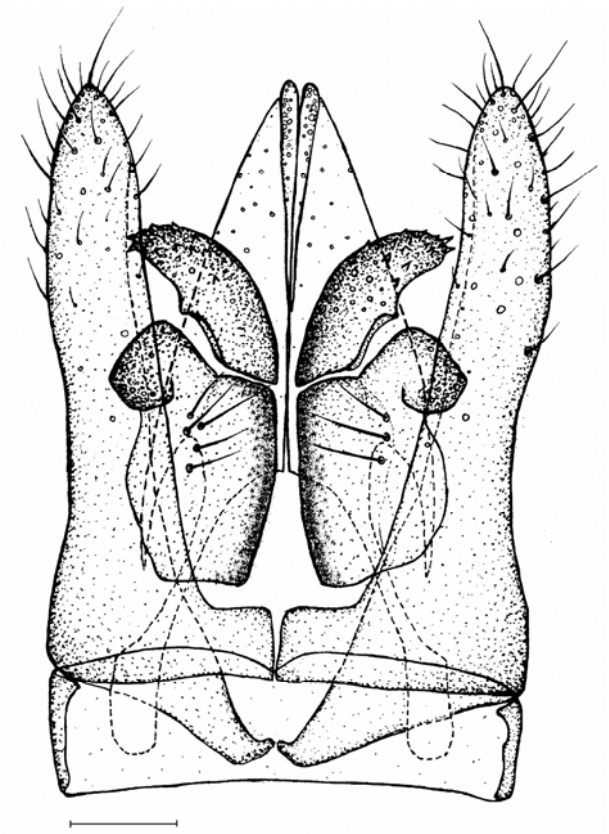

Fig. 21. Male genitalia of *Crassomicrodus medius* (Cresson, 1865). Scale bar 0.1 mm.

DISCUSSION

In the classification of certain groups of insects where it is difficult to establish the place of some taxa (primarily species), we use the characteristics of the male and female genitalia to accomplish the task. On the basis of analysis of the copulatory organs of the chosen species of Agathidinae it can be concluded that they each have a unique structure pattern. The basal ring is considerably reduced, in the form of a band, which represents without doubt a progressive trend. Indeed, this is a prominent trend within the Braconidae. Although the basal ring has a similar form in the studied species, its length is specific for each of the species, which is particularly noticeable within the genus *Agathis*. This means that this characteristic could be used for

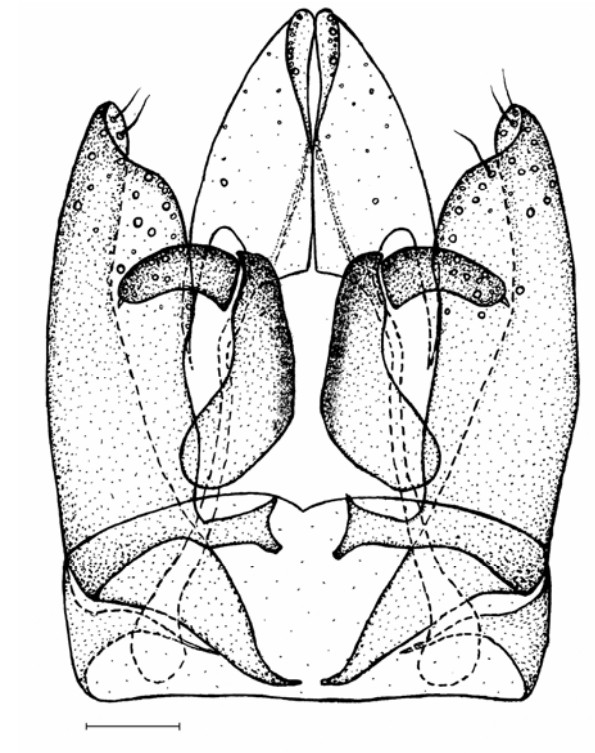

Fig. 22. Male genitalia of *Earinus gloriatorius* (Panzer, 1809). Scale bar 0.1 mm.

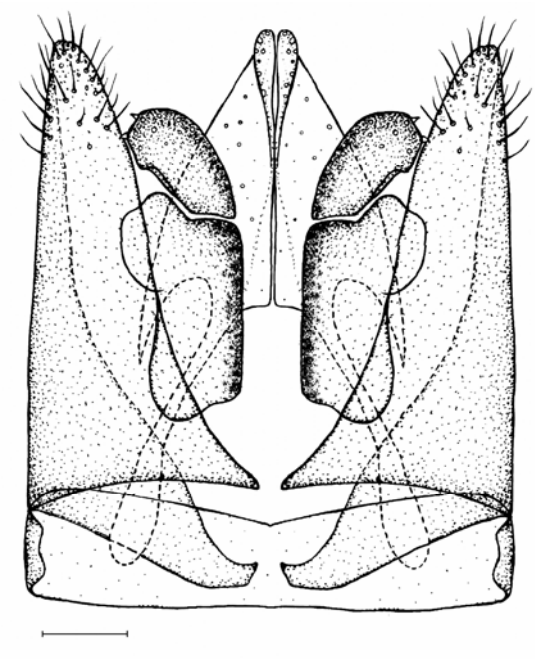

Fig. 23. Male genitalia of *Zelomorpha arizonensis* Ashmead, 1900. Scale bar 0.1 mm.

the identification of the species with great certainty. The morphological characteristics of the paramerae (form, size, and arrangement of setae) are specific for each of the species, making them reliable for use in taxonomy. Both the form and size of the volsellae slightly vary, but the degree of sclerotization of the anterior and interior margins is specific for each of the species. The cuspides of Agathidinae are generally weakly developed. It seems that there is a correlation in the degree of cuspis development and sclerotization of anterior and interior margins of the volsellae. In the species with strong sclerotization of anterior and interior margins of the volsellae the cuspides are weakly developed or absent. The evolutionary trend of the cuspides is questionable. According to Tobias (1963), the general trend is development of cuspides and their detachment from volsellar plates (basivolsellae). In accordance with this, they should not be developed in primitive groups, but Belokobiljskij (1987) observed well-

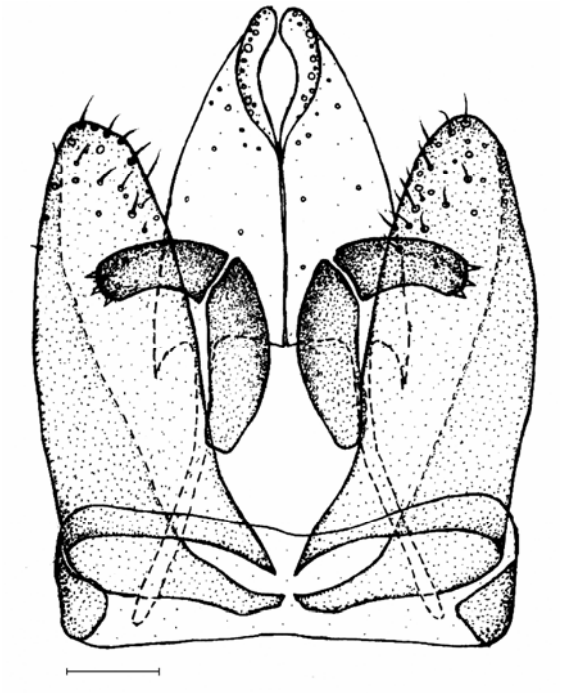

Fig. 24. Male genitalia of *Disophrys caesia* (Klug, 1835). Scale bar 0.1 mm.

developed volsellae in most Doryctinae. The morphology of the digiti is easily seen and has undoubtedly the best diagnostic value. Maeto (1996) also found both digitus and volsellar structure for intergeneric relationships within the subfamily Microgastrinae to be reliable. Considering the morphological features of the aedeagus, its valvae have little diagnostic value in that in most species their form is the same: the phallotremae are spacious, while the apodemae are mainly short, exceeding the base of the basal ring only in few of the species.

CONCLUSIONS

The male genitalia of the analyzed species of the subfamily Agathidinae have the common pattern of structure (apart from mouthparts and wing venation) by which the species from the subfamily are easily recognized. The basal ring is band-like, which is undoubtedly an apomorphic trait. The paramerae are short, widened basally and furnished with sparse setae apically. The volsellae are short, varied in length and degree of the sclerotization. The cuspides are weakly developed. The digiti vary mostly in the form and number of distal teeth. Their morphology is of the greatest diagnostical value. The aedeagi are with short valvae, broad phallotremae, and varying lengths of apodemae. The characteristics of the male genitalia may be used with great reliability for both identification of the genera and phylogenetic analyses. The diagnostic value of the male genitalia characteristics within the genus is less reliable and can be used only within multispecific genera (together with external morphology) for establishing the place of the species belonging to this subfamily.

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ГЕНИТАЛНЕ СТРУКТУРЕ МУЖЈАКА КОД ВРСТА ПОДФАМИЛИЈЕ AGATHIDINAE (HYMENOPTERA: BRACONIDAE) И ЊИХОВ ЗНАЧАЈ У ТАКСОНОМИЈИ

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У раду је приказана морфолошка анализа гениталних структура мужјака 24 врсте подфамилије Agathidinae сврстаних у 10 родова. Дат је детаљан опис ових структура код свих врста и анализирана је њихова таксономска вредност. Установљено је да морфологија гениталија мужјака може послужити за идентификацију родова, док је њена употреба на нивоу врста ограничена, осим код родова са великим бројем врста.