STUDIES ON THE *BRACON HEBETOR–BREVICORNIS* COMPLEX (HYMENOPTERA: BRACONIDÆ)

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Introduction

The rôle played by *Bracon brevicornis* Wesmael and *B. hebetor* (Say) as ectophagous larval parasites of many well-known pests is an important one. The number of hosts on which these ectoparasites have been recorded is very large indeed, as evidenced by the available literature, both in India as well as abroad. Notwithstanding the very extensive work by a multitude of entomologists done on the biology of these forms, it is not known for certain whether *B. brevicornis* and *B. hebetor* should be regarded as different species or that one is merely the variety or race or sub-species of the other. The latter is the conclusion. Puttarudriah and Channa Basavanna (1956) arrived at, on the basis of their studies of the morphological characters (genitalia included) and the experiments stated by them to have been made to interbreed the forms. However these workers, *viz.*, Puttarudriah and Channa Basavanna did not give a detailed description of the male genitalia of the two forms. Indeed the only reference thay made to the external male genitalia, of vital importance in specific determination not only in the Hymenoptera but also in most other orders of Insecta, is in the following words: "An examination of the male and female genitalia of a number of specimens of *hebetor* and *brevicornis* (inclusive of those reared on *Pyrausta* and *Nephantis*) *revealed almost no distinct difference between the two species*" (t.c.: p. 189) (Italics of the present authors).

The work carried out by the present authors seems to point to an entirely different conclusion, *viz.*, that *B. brevicornis* and *B. hebetor* are two separate or discrete species. The studies made were of two kinds: (1) morphological and (2) biological, the latter comprising the experiments conducted to find out whether the two forms interbred.

MATERIAL AND METHODS

Individuals of *Bracon brevicornis* were obtained from the culture of this parasite being maintained in the Parasite Laboratory of the Entomology Division, Indian Agricultural Research Institute, New Delhi. Early last year (1956) a few live pupæ of *B. hebetor* were received from the Division of Entomology, Mysore Agriculture Department, Bangalore, and a regular culture of this parasite is also being maintained in this laboratory since that time.

For studying the male genitalia, the cut abdominal tips were kept overnight in 10% KOH solution, washed thoroughly in water, dissected under binoculars and then mounted in Canada balsam after being passed through acetic acid and carbol-xylol mixture (3 parts xylol: 1 part carbolic acid). No staining with carbol-aniline, etc., was found necessary as the various components were sufficiently well scleritised.

As regards the hybridisation experiments, pupæ of each form were kept in separate tubes (one pupa only in one tube) and, when adults emerged, reciprocal pairs were released in small glass jars covered with muslin cloth and were provided with moistened split raisins. Two full-grown *Corcyra* larvæ were exposed to the female of each pair over a period of 24 hours. The parasitised *Corcyra* larvæ were transferred to paired petri-dishes after this period of time and fresh larvæ were exposed. This was continued till the female of each pair died.

To serve as a sort of control or check, males and females of the same species (1♂ *hebetor* × 1♀ *hebetor*, 1♂ *brevicornis* × 1♀ *brevicornis*) were also paired and provided with *Corcyra* larvæ. The progeny developing on the *Corcyra* larvæ in both sets of experiments were studied as to the sex of the individuals. All experiments were conducted at 25° C. and 70% R.H.

MORPHOLOGICAL STUDIES

(*A*) *Colour characters*

A study of the colour characters of about two hundred individuals each of the two forms showed that no great reliance could be placed on these characters. Richard and Thomson (1932), Cherian and Margabandhu (1949) arrived at the same conclusion as this during the course of their studies. This is not surprising since the inadequacy of chromatic difference and variations has been demonstrated in many other groups of the Insecta. Moreover, as Narayanan *et al.* (1954) showed, even ontogenetic colour changes can be induced in the case of *B. brevicornis* by subjecting the pupæ to different temperatures.

(*B*) *Number of antennal segments*

(1) *B. hebetor*.—(*a*) Males—From Table 1 A (*i*) it will be seen that the highest number of antennal segments in a single individual was 25,

TABLE I A

B. hebetor

(i) Males		(ii) Females	
Antennal segments	Number of specimens	Antennal segments	Number of specimens
25	4	18	5
24	39	17	45
23	25	16	0
22	8	15	0
21	4	..	..
20	3	..	..
Total number in the lot examined ..	83	Total number in the lot examined	50

among the specimens examined by the authors, while the lowest was 20. Table 1 C: A shows the number of males with an unequal number of anten na segments.

(*b*) Females—The highest number of antennal segments for a single individual was 18, while the lowest number was 17. Out of 50 specimens examined only 5 had 18 antennal segments: the others had only 17 [Table I A (ii)]. Of the 50 females examined, none showed a difference in the number of segments between the two antennæ (Table I C: B).

TABLE I B

B. brevicornis

(i) Males		(ii) Females	
Antennal segments	Number of specimens	Antennal segments	Number of specimens
25	0	18	0
24	3	17	8
23	25	16	27
22	30	15	9
21	4	..	..
20	2	..	..
Total number in the lot examined ..	164	Total number in the lot examined ..	44

(2) *B. brevicornis*.—(*a*) Males—From Table I B (i) it will be seen that the highest number of antennal segments in a single individual was 24, and the lowest number was 20. The majority of specimens had 22 segmented antennæ.

(*b*) Females—It is seen from Table I B (ii) that none of the females had more than 17 segments in the antenna, while the lowest number of antennal segments in an individual was 15. The majority of individuals had 16 antennal segments.

(*C*) *Male genitalia*

(*a*) *B. hebetor*.—The entire male genitalia of this species are illustrated on Plate II, Fig. 1, while the phallus (as separately dissected and mounted) is shown in Plate II Fig. 2.

TABLE I C

B. hebetor: A. Males

Total number of specimens examined	Number of individuals with unequal number of segments in the two antennæ			
	Number of segments in the right antenna	Number of segments in the left antenna	Number of segments in the right antenna	Number of segments in the left antenna
83	24	23	22	21
	23	24	21	20
	23	24	24	23
	22	23	25	24
	23	24	21	22
	22	23	22	23
	23	24	24	25
	24	23	22	20
	22	23	22	23
	23	22	24	23

B. Females

Total number of specimens examined	Number of individuals with unequal number of segments in the two antennæ
50	Nil

(*b*) *B. brevicornis.*—The male genitalia are illustrated on Plate II, Fig. 3 and the phallus is separately illustrated in Plate II (Fig. 4).

Since the authors propose to describe the male genitalia of not only these two forms but also of other available species of the genus *Bracon* Fabricius, both Indian and exotic, elsewhere in detail, exhaustive descriptions of the male genitalia of the two forms are not given here. However, the illustrations clearly show the salient and quite marked differences between the male copulatory organs of the two forms not only in the gross parts but also in a minute component, like the phallus.

(*D*) *Wings*

The fore and hind wings of *B. hebetor* are illustrated on Plate I, Figs. 1–2 and those of *B. brevicornis* in Figs. 3–4.

BIOLOGICAL STUDIES

The details of the experiments to find out whether the two forms mated to produce a " bi-sexual " progeny or not have been described earlier in this paper. In addition to these experiments, males and females of the same

TABLE I D

Bracon brevicornis: A. Males

Total number of specimens examined	Number of individuals with unequal number of segments in the two antennæ			
	Number of segments in the right antenna	Number of segments in the left antenna	Number of segments in the right antenna	Number of segments in the left antenna
164	20	21	22	23
	21	22	23	22
	21	22	21	22
	23	22	23	22
	23	22	20	19
	22	23	22	23
	23	22	..	..

B. Females

Total number	Number of individuals with unequal number of segments in the two antennæ	
	Number of segments in the right antenna	Number of segments in the left antenna
44	16	17
	15	16
	17	16
	17	16
	17	16
	15	16

form were also caged together and their progeny examined. These latter experiments, as explained earlier, were designed to serve as 'controls' for the experiments to find out whether the two forms interbred successfully.

The results of the 'reciprocal-cross' experiments are contained in Table II: 1, while those of the 'controls' are shown in Table II: 2. It will be seen from Table II: 1 that the progeny of all the reciprocal crosses was purely males, whereas females were present in some numbers in the progeny of the crosses of the same species (Table II: 2).

Discussion of the Results Obtained

Puttarudriah and Channa Basavanna (1956) made the following statement, while reviewing the extant literature on the host range of the two forms: "Richards and Thomson (1932) reviewed the host records of the two species and it is interesting to note that, while giving the synonymy of *B. hebetor*, *B. brevicornis* was also included though they considered the latter separately and regarded it as established that *B. hebetor* is mainly a domestic species and *B. brevicornis* lives out of doors with of course a few exceptions in both cases" (t.c.: p. 183).

Puttarudriah and Channa Basavanna seem to imply that by including the *brevicornis* of certain authors in the synonymy of *hebetor* Say, Richards and Thomson synonymised *hebetor* and *brevicornis* out right. A more careful study of that part of the work by Richards and Thomson (1932) (p. 225) shows that what the authors meant was merely this: that certain authors [like Kirby (1884), Schmiedeknecht (1896), etc.] record as *brevicornis* certain forms which should be more correctly assigned to the species *hebetor*. Hence there was nothing unusual or 'interesting' about this part of the paper by Richards and Thomson (1932).

The number of antennal segments has been regarded as one of the chief criteria on which the two forms can be separated—for example, in the keys given by Muesebeck (1925) who stated that in *hebetor* the antenna of the female had 13 to 15 segments and that of the male had 18 to 23 segments, while in *brevicornis* the corresponding numbers were 17 to 19 ("very rarely 16-segmented") and 20 to 27. Lal (1947) stated in this connection: "The table of characters (as given in Muesebeck's key) for *hebetor* should stand, but for *brevicornis* the antennal segments in the female may range from 16 to 21 (t.c.: p. 88). However, there is reason to believe that there is considerable variation in the number of antennal segments, both in the male and female in the family Braconidæ, particularly in species and genera with a comparatively large number of antennal segments as is the case with the genus *Bracon* Fabricius.

TABLE II

Cross		Number of progeny	Sexes: Males	Sexes: Females	Cross		Number of progeny	Sexes: Males	Sexes: Females
Hebetor ♂ ..	1.	30	30	0	*Hebetor* ♂ ..	1.	15	8	7
Brevicornis ♀ ..	2.	25	25	0	*Hebetor* ♀ ..	2.	13	9	4
	3.	20	20	0		3.	12	9	3
	4.	26	26	0		4.	20	12	8
	5.	16	16	0		5.	22	15	7
	6.	13	13	0		6.	19	14	5
Hebetor ♀ ..	1.	24	24	0	*Brevicornis* ♂ ..	1.	20	10	10
Brevicornis ♂ ..	2.	22	22	0	*Brevicornis* ♀ ..	2.	22	14	8
	3.	14	14	0		3.	11	7	4
	4.	16	16	0		4.	17	12	5
	5.	21	21	0		5.	18	14	4
	6.	28	28	0		6.	19	10	9

The results of the observations made on this point by the present authors are, however, very dissimilar to those of both Muesebeck (1925) and Lal (1947). We found that in *hebetor* the majority of the females had 17-segmented antennæ and only 5 out of 50 females had 18-segmented antennæ, whereas in the males the highest number of antennal segments was 25 (4 males out of 83 examined) and the lowest number was 20, the majority being with 24-segmented antennæ. As regards *brevicornis* the present authors observed that the highest number of antennal segments in the female was 17 (8 out of 44 females examined), the lowest number 15 (9 out of 44 females examined), the majority of the females being with 16-segmented antennæ, whereas in the males of the same species (*brevicornis*) the highest number of antennal segments was 24 (3 out of 164 males examined), the lowest number 20 (2 out of 163 males examined), the majority of the females being with 22-segmented antennæ.

Our observations confirm those made earlier by Puttarudriah and Channa Basavanna (1952), regarding the inequality of the number of the segments in the two antennæ of the same individual of a species. Two lots of specimens of the two species were examined and Tables I C & I D give an idea of the results obtained. It will be seen that quite a fair percentage of the specimens examined displayed this inequality. From Tables I C: A & B and I D: A & B an idea of the relative preponderance of this inequality of segmented is seen with respect to the two sexes.

Some other interesting observations were made by the present authors regarding antennal characters in the two species. They are briefly: (1) That the number of antennal segments is not directly correlated with the size of the individual. Thus some specimens has as many as or even more antennal segments than specimens appreciably bigger than them in size. (2) The inequality in the number of antennal segments in the two antennæ of the same individual was often traceable to a partial fusion of two neighbouring segments or rather their imperfect delimitation during development.

However, there were specimens in which this segmental inequality was due to a segment being clearly less in one antenna as compared to the other and not due to incomplete or partial fusion of two segments. Another interesting observation we made was that while in *hebetor* the inequality between the number of segments of the two antennæ of the same individual was very rare in the males but quite frequent in the females. While in case of *brevicornis* it was as frequently encountered in the males as in the females. (Tables I C: A, B & I D: A, B).

In view of the foregoing, Muesebeck's key used, with slight modifications, so far to distinguish *hebetor* and *brevicornis* does not seem to apply fully at least to the large number of specimens examined during the course of the present investigations. We are not sure as to how to explain the difference in the results obtained in this regard by Muesebeck and those obtained by us. The same applies with equal force to the results obtained by Puttarudriah and Channa Basavanna (1956).

As regards the external male genitalia (Plate II, Figs. 1–4), the two species differ in the shape of the basal ring, the volsellar plates and the phallus—which, in each case, was carefully separated and mounted individually.

The wings of the two species (Plate I, Figs. 1–4) show considerable individual variation, especially in regard to the extent to which M_1, m—M_2 and M are marked. An interesting observation made was the " sexual dimorphism " obtaining in both the forms in regard to the degree of differentiation of the vein M. In the males of both the forms, this vein (M) was appreciably less marked than in the case of the females. The venation of the two forms is very similar, but the wings of *B. hebetor* are somewhat narrower and more elongated than those of *B. brevicornis.*

Our experiments to find if *hebetor* and *brevicornis* can interbreed, yielded only negative results, inasmuch as the progeny of each of the 12 reciprocal crosses was all male. In contrast to this, males and females of either species when paired produced both males and females in their progeny, under the same conditions of temperature and humidity (25° C. and 75% R.H.). It may be stated in this connection that there were repeated attempts at copulation in the individuals of the reciprocal crosses, though such attempts were obviously futile, inasmuch as the resulting progeny was only males.

The present problem is admittedly complexer than what it seems to be. We had sent the manuscript of this paper to Dr. C. F. W. Muesebeck, Washington Museum, who is the world's foremost authority on the family Braconidæ. He made some comments thereon which we are reproducing below with his kind permission.

" The problem is a most interesting one, and I thank you for the opportunity of examining your manuscript, although I am very much perplexed by the data you have presented. It is difficult for me to believe that you had the true *hebetor* in your experiments. Say's type had 14- segmented antennæ, and in long series available to me here (including material from various parts of the world, and from such hosts as *Ephestia*, *Plodia* and *Sitotroga*) the vast majority of females have 14 segments; many more have 13 segments in the antennæ than 15, and only three specimens of the very large number examined have 16. From the data you have presented I would be inclined to consider all your material to be *brevicornis* or segregates of that species. Dr. R. I. Sailer, of our staff, who has been conducting genetic studies in Hemiptera for several years, and to whom I showed your manuscript, suggested that there may be several sibling species in this *hebetor-brevicornis* complex with varying degrees of reproductive isolation.

Wesmael's type of *brevicornis* has 17-segmented antennæ, and the males in his type series have the antennæ 20 to 26-segmented. Our material of *brevicornis* from Europe agrees beautifully with the type series. In the female sex the number of antennal segments ranges from 16 to 18, most of the specimens having 17 or 18; in the males the antennæ are 20 to 26-segmented as in the types. In view of this I am somewhat confused by the numerous specimens I have examined that were reared in India from the pink bollworm and from *Chilo zonellus*. These series seem to be intermediate between *hebetor* and *brevicornis*. In more than 70% of the females the antennæ are 16-segmented; in less than 5% are they either 14-segmented or 17-segmented. Though obviously intermediate the females seem to approach *brevicornis*; but the males are more like *hebetor*, having the antennæ 21 or 22-segmented. It is quite possible, of course, that the apparent differences represent host influences."

From the above-quoted remarks of Dr. Muesebeck's it is clear that there is some ground to doubt the true identity of the *hebetor* specimens involved not only in our own experiments and observations but also in those of Puttarudriah and Channa Basavanna (1956). Say's type of *hebetor* had 14-segmented antenna, and Muesebeck himself states that the majority of the females examined by him had 14-segmented antenna, quite a few had 13, and only a very few had 15 or 16-segments. This is at variance with our observations as also those of Puttarudriah and Channa Basavanna (Table III, p. 188 t.c.).

In view of this, we are constrained to remark that either the original *hebetor* has undergone a large number of mutations and has started showing considerable variation in various morphological characters after having spread to many different climes since it was first described by Thomas Say; or that the species used by Puttarudriah and Channa Basavanna and ourselves is not the true *hebetor*, but is a yet unidentified sibling species from amongst the *hebetor-brevicornis* complex very near the true *hebetor*. It is interesting to note in this connection that this species was identified as *hebetor* by the Commonwealth Institute of Entomology according to Puttarudriah and Channa Basavanna (t.c.: p. 190) and that we got some live pupæ of this species from Dr. Puttarudriah and it was from this nucleus that a culture was begun in our laboratory.

The passages quoted from Dr. Muesebeck's letter to one of us (E. S. N.) also show the existence of very considerable variation in the number of antennal segments of *brevicornis* as well. How far these differences represent host-influences is beyond the scope of the present work, but we might add here that the *brevicornis* culture being maintained in our laboratory on *Corcyra cephalonica* was started from material identified by Dr. Muesebeck in the year 1954.

In view of the foregoing discussion we have but to admit that the present investigations are only a contribution towards the solution of the admittedly very interesting but puzzling problem of the *hebetor-brevicornis* complex. Light may be thrown on this by a future study of the chromosomes of the species concerned. Such a study will also be, in a way, the final word on the identity of discreteness of *B. hebetor* and *B. brevicornis*. This is not surprising in view of what Muesebeck himself wrote in 1925 regarding the genus *Bracon* (or *Microbracon* Ashmead, as it was then known): " In few groups of the Braconidæ is there found so wide a range of variation within species as in *Microbracon*. Practically all characters, many of them excellent characters in other groups, vary greatly in this genus " (t.c.: p. 5).

SUMMARY

This work discusses the views of various authors as to whether *Bracon hebetor* (Say) and *Bracon brevicornis* (Wesmael) are two separate species.

The fairly detailed studies made during the course of the present investigations in regard to the antennæ, the external male genitalia and the experiments conducted to find if the two forms successfully mated to give rise to a progeny consisting of both males and females, have been made. The inequality in the number of antennal segments in the individuals has been studied in detail. It is suggested that there is a complex of more than two species and only a thorough cytological study could solve the problem.

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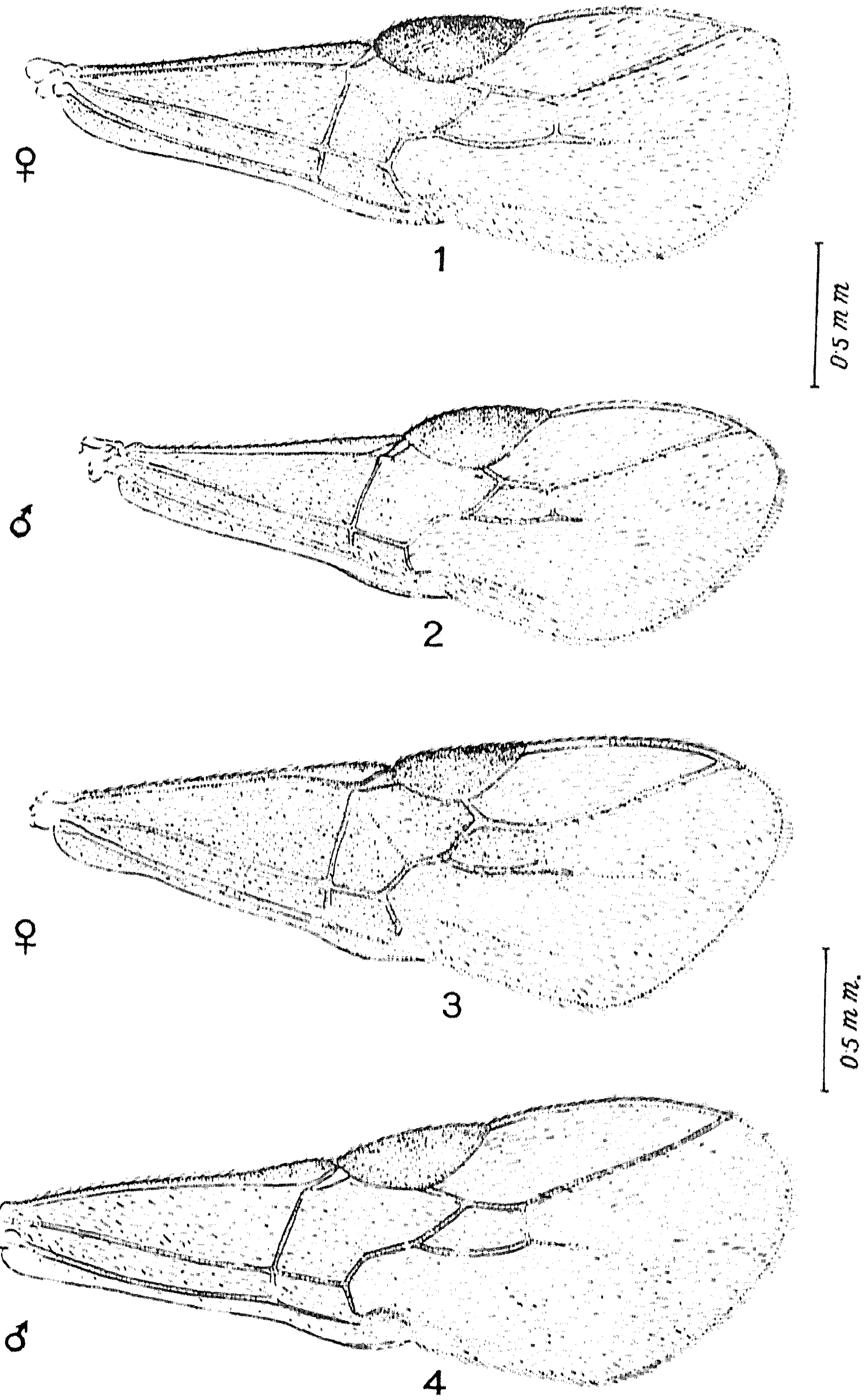
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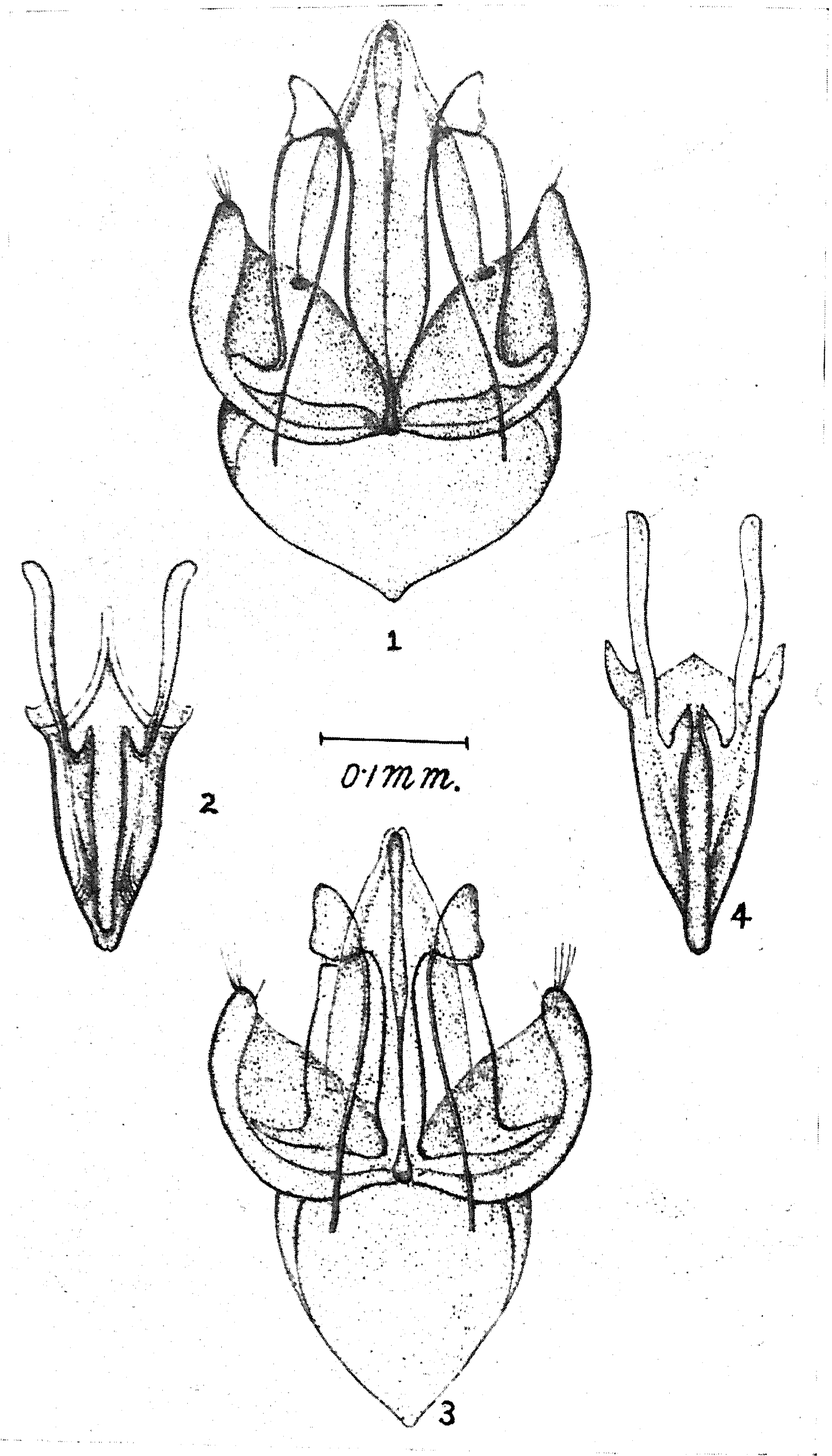
Bracon hebetor

Bracon hebetor

Bracon brevicornis



Bracon brevicornis

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Explanation of Plates

Plate I

Fig. 1. Fore wing of *Bracon hebetor*, female.

Fig. 2. Fore wing of *Bracon hebetor*, male.

Fig. 3. Fore wing of *Bracon brevicornis*, female.

Fig. 4. Fore wing of *Bracon brevicornis*, male.

Plate II

Fig. 1. Male genitalia, *Bracon hebetor*.

Fig. 2. Phallus, *Bracon hebetor*.

Fig. 3. Male genitalia, *Bracon brevicornis*.

Fig. 4. Phallus, *Bracon brevicornis*.