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Revision of *Microtylopteryx* Rehn 1905 (Orthoptera, Acrididae, Ommatolampinae)

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Abstract

Rehn's (1955) two subgenera *Microtylopteryx* (*Microtylopteryx*) and *Microtylopteryx* (*Tristanacris*), each comprising several species and subspecies, are here each considered to represent a single species, *M. hebardii* Rehn 1905 and *M. fusiformis* Rehn 1905 respectively. I arrive at this conclusion on the basis of a) the genital anatomy, and b) morphometric analysis of all the previously named taxa and several previously unsampled populations. There are no differences within each of these taxa in internal or external genital structure. In the morphometric analysis, measures specifically designed to correspond to Rehn's diagnoses were used, and new material was collected from the various type localities to supplement the original material. The results show that the original diagnoses, which were based on small samples, do not adequately represent the populations from which the type series were drawn.

Virtually every geographically circumscribed population which has been investigated differs from the rest, often significantly, in the average of one or more quantitative characters. However, the degree of overlap between the different populations in the range of these characters is typically very large, and often complete, and individual specimens therefore cannot be allocated reliably to particular populations on the basis of their morphology. All such overlapping populations are here considered to belong to a single taxon. Where, exceptionally, there is no overlap between populations in some character, and individuals can be reliably allocated to a specific population on its basis, subspecific ranks have been allocated.

Within *Microtylopteryx* (*Microtylopteryx*), *M. hebardii caligo* Rehn is synonymized with *M. hebardii* Rehn, and *M. nigrigena* Hebard is relegated to subspecific rank as *M. hebardii nigrigena*. Within *M. (Tristanacris)* two species (*talamancae* Rehn, *tristani* Rehn) and one subspecies (*fusiformis lamprus* Rehn) are synonymized with *M. fusiformis* Rehn. *M. worthi* Rehn and *M. chiapensis* Rehn are relegated to subspecific rank within *M. fusiformis*, and one further new subspecies (*M. f. fastigiata* n. ssp) from Western Panama is erected. Each of Rehn's subgenera thus becomes monospecific, and it is suggested that the division into two subgenera is now redundant.

A key to species and subspecies is given, and distribution maps.

Key words

Grasshoppers, taxonomy, Neotropics, Acrididae, Ommatolampinae, morphometrics

Introduction

Microtylopteryx was erected by Rehn (1905) for the two species *fusiformis* and *hebardi*, both of which he had collected in Carrillo, in the foothills of the northern Caribbean lowlands of Costa Rica. *M. hebardii* is the type species of the genus. Hebard (1924) described from the then Panama Canal Zone the species *nigrigena*, which is very similar to *hebardi*. Subsequently Rehn (1929) described from the Pacific drainage of the Meseta Central of Costa Rica, the subspecies

fusiformis lamprus, and the species *M. tristani* from the surrounding mountains; from the Estrella valley in the southern Caribbean lowlands of Costa Rica he further described *M. talamancae*. In 1955, Rehn described a mountain subspecies of *hebardi* (from the same type locality as *tristani*), *M. h. caligo*. In the same paper he divided the genus into two subgenera, *Microtylopteryx* (*Microtylopteryx*) for *hebardi* and *nigrigena*, and *Microtylopteryx* (*Tristanacris*) for the species *fusiformis*, *talamancae* and *tristani*, which he had previously referred to collectively as the *fusiformis* species group. He also described two further new species of *M. (Tristanacris)*, *M. worthi* from Northern Honduras and *M. chiapensis* from Southern Mexico.

On the basis of prolonged field acquaintance with the Costa Rican and Panamanian populations of these insects, I have long felt that Rehn was too divisive in his taxonomy. While there is no question that *M. hebardii* and *M. fusiformis*, in the sense of his 1905 paper, are discrete taxa, one may have considerable doubt about his later subdivisions of them, particularly his treatment of the subgenus *Tristanacris*. His descriptions were based on small samples — at the extreme, *M. chiapensis* was based on a single male, and *M. f. lamprus* was based on two males, one of which he described as "atypical" — and casual inspection of a large collection from any given locality makes it obvious that the species is quite variable in size, color and pattern and a number of morphological characters, including the shape of the fastigium in dorsal view and the degree of indentation of its tip, the profile of the frons and vertex, and the profile of the pronotal medial carina, all of which are characters Rehn used in his diagnoses. Superimposed on this is considerable variation between populations. *M. hebardii* occurs over a large altitudinal range on the Caribbean slope, from sea level to at least 1600 m altitude at Alto la Palma. *M. fusiformis* s.l. is a wide-ranging taxon extending from Central Panama on both the Atlantic and the Pacific slopes to at least Southern Nicaragua, and from sea level to at least 2300 m altitude on Volcán Barba. Furthermore, both species are flightless; some local differentiation is therefore to be expected and indeed can be demonstrated, most obviously in overall size.

It is evident that Rehn himself entertained some doubts, as he wrote (1929: 54): "This species (i.e., *M. talamancae*) shows an appreciable amount of variation in color tone, size, ... and to a degree in the fastigial angle and pronotal outline as seen in profile. These fluctuations however are paralleled in *M. fusiformis* and are no greater than those found in the latter species It is possible that the future may show *M. talamancae* to be subspecifically connected with *M. fusiformis*, but without material clearly demonstrating this ... I prefer to consider them specifically distinct".

Within the subgenus *Tristanacris*, Rehn defined only *M. worthi* with clear characters — it is larger than the rest and its tegmen is only one third as long as in other forms. Rehn's characters for the other taxa are hard to pin down. Appendix 1 gives the significant features of his keys and descriptions. Most are of the form "more concave (*etc.*) in taxon A than in taxon B", and demand a comparison to be realized. In this revision I have therefore attempted to use statistical morphometrics to test Rehn's taxonomic hypotheses, deriving mathematical ratios corresponding as closely as possible to his characters.

I have also used the internal genitalia in this analysis. They have not been examined previously, except at the generic level by Amédégno (1977).

Materials and methods

Populations Studied

Microtylopteryx (*Microtylopteryx*):

- a) the type series of *hebardei* (Carrillo, S. José, Costa Rica);
- b) a supplementary sample from the lower Sarapiquí valley, Heredia, Costa Rica;
- c) a sample from the Cordillera del Norte, Costa Rica;
- d) the type series of *hebardei caligo*, Alto la Palma, S. José, Costa Rica;
- d) the type series of *nigrigena* (Gatún, Colón, Panama);
- e) new material of *nigrigena* from Cerro Copé, Coclé, Panama.

Microtylopteryx (*Tristanacris*):

- a) the type series of *fusiformis* (Carrillo, S. José and Guapiles, Limón, Costa Rica);
- b) a supplementary sample from the Carrillo neighbourhood and the lower Sarapiquí valley, Costa Rica;
- c) the type series of *talamanca* from the Valle de la Estrella, Limón, Costa Rica;
- d) a supplementary series from the Valle de la Estrella;
- e) the type series of *tristani* (Alto la Palma, Costa Rica, and other localities);
- f) a supplementary sample from the same localities as the type series of *tristani*;
- g) the type series of *fusiformis lamprus* (nr S. José, Costa Rica) and another individual from near the type locality;
- h) a sample from the Cordillera del Norte, Costa Rica;
- i) a sample from S.W. Costa Rica;
- j) a sample from Changuinola, Bocas del Toro, Panamá;
- k) a sample from Wekso, Río Teribé, Bocas del Toro, Panamá;
- l) a sample from Alto la Piedra, Veraguas, Panamá;
- m) a sample from El Volcan, Chiriquí, Panamá;
- n) a sample from the highlands of Bocas del Toro;
- o) a few specimens from Eastern Nicaragua;
- p) the type series of *worthi* (Tela, Atlantida, Honduras);
- q) a supplementary population from Tela;
- r) a sample from Progreso and La Muralla (Atlantida, Honduras);
- s) the type of *chiapensis* and two other specimens from Chiapas, Mexico;
- t) a sample from Yepocapa, Guatemala.

Further details of each population are given in the text.

Genitalia

The internal genitalia of males and females were extracted, macerated in NaOH solution, stained in acid fuchsin, and examined microscopically, using standard techniques.

Morphometric analysis

Procedure and definitions.—The strategy adopted here is to characterize the previously described taxa statistically, and to compare them with each other and with samples from other areas. Rehn's original material, including most of his paratypes, is preserved in the ANSP, and is available for this purpose. Most of his taxa are however based on too few specimens for statistical analysis. As they are vaguely defined and difficult or impossible to recognize morphologically, I adopted a topotypic approach, supplementing his type series using modern samples collected from his type localities or nearby areas, until samples of a sufficient size for statistical analysis were obtained. Material from other localities was then incorporated into the analysis at a later stage.

When any two of these geographically defined populations are compared, it is usually found that they differ significantly in the mean of one or more quantitative characters. Typically, however, the populations overlap largely or completely in the range of these characters. Under these circumstances an individual specimen cannot be allocated with certainty to either population, and I take this to be an indication that the two populations belong to the same taxon, or at least, cannot be usefully split into two taxa. Such a pair of populations would then be pooled, and used to compare with the next candidate taxon.

In the event that a geographically defined population possesses a character which discriminates all its individuals from other populations, then this population is considered to be a separate taxon. In the absence of genital differentiation, I consider it to be a subspecies, as the Ommatolampinae in general have well differentiated male genitalia.

Dimensions and ratios used.—The following dimensions (see also Fig. 1) were measured to 0.02 mm with a digital micrometer stage and a 10× ocular fitted with cross-hairs, under 12× to 50× total magnification.

P — Length of the pronotum in the midline.

L — Overall length from the tip of the fastigium to the most posterior part of the genitalia, measured in lateral view.

Ant — Length of the antennal flagellum (*i.e.*, excluding scape and pedicel).

IOS — Interocular space at its narrowest point.

E-E — The maximum width across the eyes in dorsal view.

Fast B — Breadth of fastigium. Rehn does not say how he measured this. I measured from the outer margins of the two lateral ocelli, which are visible on the edges of the fastigium in dorsal view in this taxon.

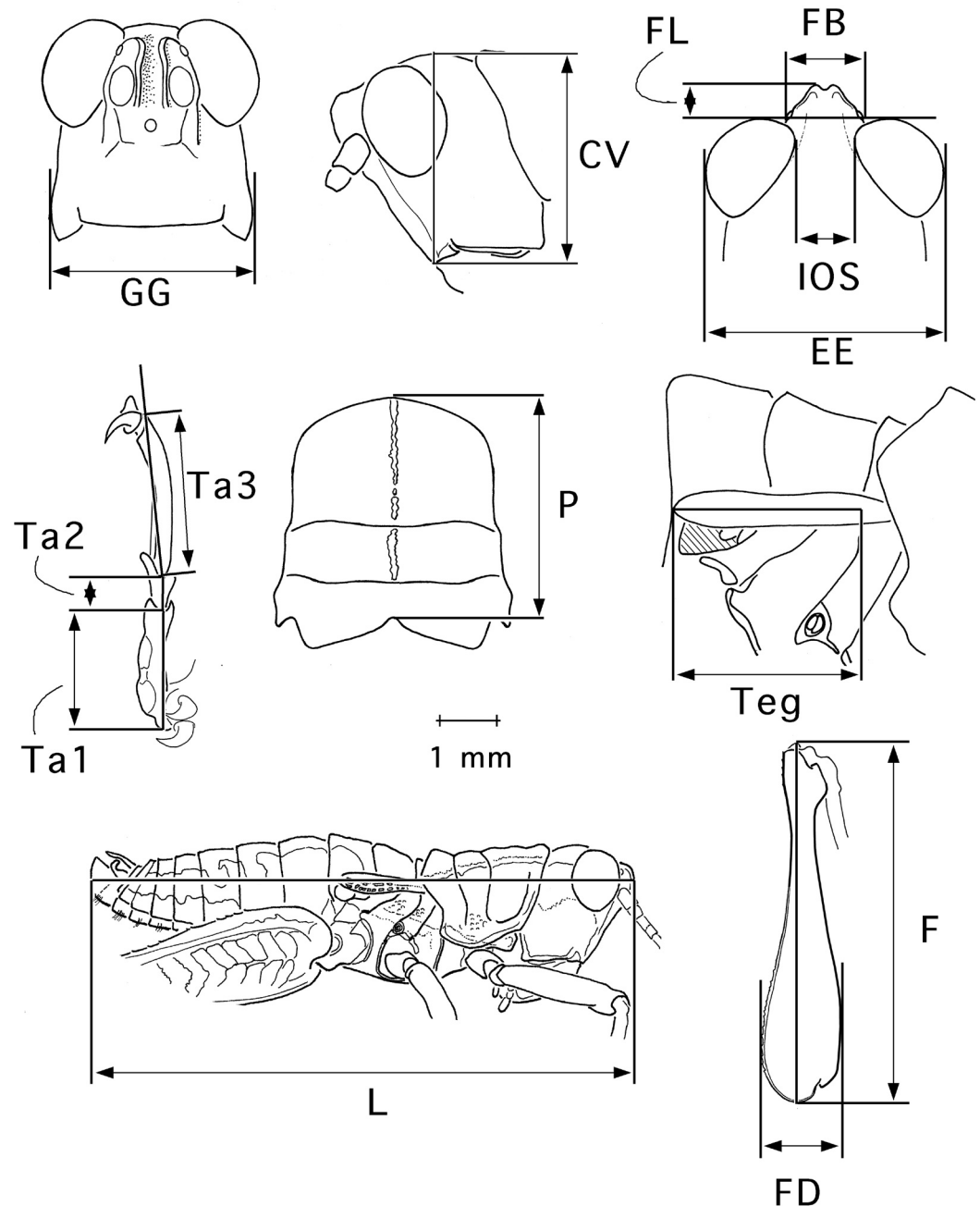
Fast L — Length of fastigium. Measured from a line joining the most anterior part of the profile of the eyes in dorsal view, to the tip of the fastigium.

C-V — Height of head from clypeal suture to vertex. Measured in lateral view from the clypeal suture to the highest point on the vertex posterior to the eyes.

G-G — Maximum width across the genae in frontal view.

F — Maximum length of hind femur.

Fig. 1. Anatomical sketches of *M. hebaridi* to show the dimensions measured for morphometric analysis. Abbreviations defined in text pages 2-4.



FD — Depth of femur. Measured as the distance between the two parallel lines running through the dorsal and ventral extremities of the femur, drawn parallel to the long axis of the femur.

Teg — Length of tegmen. Defined as the distance between the point where the leading edge crosses the suture between the meso- and metathoracic pleura and the tip of the tegmen. (I normally prefer to use the suture between the mesothoracic epimeron and episternum, which corresponds more closely to the true base of the elytron, but it was clear from Rehn's measures that he had used the former criterion, which indeed is easier to apply in most specimens, as the latter point of measurement is usually hidden under the posterior edge of the pronotum. To convert Teg as given here to the approximate true length of the tegmen, multiply by 1.17 to 1.22, for all taxa).

Ta1, Ta2, Ta3 — The lengths of the three hind tarsal segments, measured as shown in Fig. 1. From these was calculated the sum Ta1-3.

Ta1-3 — The sum of Ta1, Ta2, and Ta3, giving a measure of the length of the hind foot (NB, without considering the arolium or claws).

The dimension P was used as a reference point. The physical size of an individual was assessed by P (and of a population by the mean of P). All the other dimensions listed above were then normalised by being divided by P for each individual (i.e., L/P, Ant/P, IOS/P, etc). These quotients correspond to the relative size of the measured characters, and permit a comparison between individuals or populations irrespective of the actual size of the specimens.

Additionally, the following ratios were calculated for each individual; these correspond to aspects of the general shape of the insect, and are therefore referred to below as "shape ratios":

F/FD — Ratio of length of femur to its maximum depth. This expresses the relative slenderness of the femur.

Ta1-3/F — The ratio of the length of the hind foot to the length of the hind femur.

Fast L/B — Ratio of the length of the fastigium anterior to the eyes to the breadth of its base. This ratio is designed to correspond to Rehn's "fastigium long and narrow" or its opposite.

C-V/G-G — This ratio measures the height of the head relative to its width. It was designed to correspond to Rehn's character "head slimmer or less slim".

E-E/G-G — The ratio of the width across the eyes to the width of the head. This ratio is designed to correspond to Rehn's "eyes more or less protuberant".

Ta1/(Ta1-3), Ta2/(Ta1-3), and Ta3/(Ta1-3) — These ratios correspond to the percentage of the total length of the hind foot contributed by each tarsal segment. Together they make up the "foot formula". Thus, a formula of 37:13:50 would indicate that the first tarsal segment made up 37% of the hind foot, the second segment 13% and the third 50%.

For all the above dimensions and ratios the minimum value, maximum value and average value were calculated for each population. For all averages with a sample size of 10 or more the standard deviation was calculated. The relative variability of characters was compared by the ratio (standard deviation/mean). Populations were compared using Student's t-test for differences of means of small samples, implemented in MS Excel. Where individual measures were being compared with a large sample, I assumed a normal distribution of the latter, allowing the assumption that 1.96 standard deviations either side of the mean includes 95% of the population.

In addition to the above measures, the number of external and internal spines on the hind femur were also counted in each individual. There is considerable variation in the size of the most proximal spines; I counted a spine as being present if it protruded at all in lateral view, regardless of its size. The numbers of tibial spines were expressed as the median for the population, this being a discrete measure rather than a continuous one.

Sexual dimorphism within populations was assessed by comparing the averages of the above measures for the two sexes. The ratio $P_{\text{male}}/P_{\text{female}}$ was taken as the standard: deviations between this ratio and other measures (e.g., $F_{\text{male}}/F_{\text{female}}$) were taken to indicate a dimorphism in relative proportions. Thus, if the pronotal ratio was 0.75 and the femoral ratio 0.85, it would be concluded that the male had relatively longer femora than the female. When normalised values or shape ratios were compared in this way, an absence of sexual dimorphism was indicated by a value of around 1.0; significantly larger or smaller values indicate sexual dimorphism.

Data repository. — The data and their analysis are too voluminous for publication here. In Appendices 2 and 3 single summary spreadsheets are presented as examples of the methodology outlined above. The results of the remaining spreadsheets are merely summarised in the text. A complete data set is available from the author on demand, and a CD-ROM copy has been deposited with the Orthopterists' Society.

Errors and uncertainties in measurement. — To assess the degree of uncertainty in measurement a sample of 14 individuals of *M. hebardii* was measured and tabulated twice, at an interval of 3 mo., and the results then compared. Of the 210 (14 × 15) measurements, 21 (10%) showed a deviation of more than 5% between the two estimates. As might be expected, these instances were predominantly in the two smallest dimensions, the second tarsal joint (Ta2) and the length of the fastigium (Fast L), both of which are in the order of 0.3 to 0.5 mm; a 5% error here corresponds to a distance of only 15 to 25 µm. These two dimensions are thus the most prone to

error, and the standard deviations calculated here are likely to be too high; there is however no reason to suppose that their means are erroneous. The remaining measures and their variances can be considered reasonably accurate.

The length of the antennal flagellum (Ant) shows considerable variability (standard deviation 9 to 13% of the mean). This must be partially due to difficulties of measurement (the antenna is rarely straight in a dried specimen), but most of it represents real biological variation.

The overall length of the animal (L) should be a rather unsatisfactory variable, not because of difficulties of measurement, but because the abdomen is frequently flexed upwards to various degrees in the male or, in the female, the ovipositor valves are either retracted or protruded or the abdomen is more or less distended with eggs. Despite these considerations, the recorded variability is not high (the standard deviation is only 4 to 5% of the mean, comparable to completely unproblematic measures such as the length of the femur (F), where it is 3%).

Abbreviations of repositories

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
CAS	California Academy of Sciences, S. Francisco, California, USA.
GBFM	G.B. Fairchild Museo de Invertebrados, Universidad de Panamá, Panamá.
INBC	Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.
MHNG	Museum d'Histoire Naturelle, Genève, Switzerland.
MNHN	Museum National d'Histoire Naturelle, Paris, France.
MUCR	Museo de Entomología, Universidad de Costa Rica, Costa Rica.
MZHU	Museum of Comparative Zoology, Harvard University, Boston, Mass., USA.
RC	The author's collection.
STRI	Smithsonian Tropical Research Institute, Panama City, Panama.
UCR	Entomological Museum of the University of California at Riverside, California, USA.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.
USNM	American National Museum of Natural History, Washington DC, USA.
USUL	Biology Museum, Utah State University at Logan, Utah, USA.

Results

I. Analysis of populations

Subgenus *Microtylopteryx*

A. Internal and external genitalia. — These were examined in all the populations discussed below. Within this subgenus no significant differences in genitalia were found. The genitalia are illustrated in the taxonomic section below.

B. Morphometry.—

Costa Rican populations

Microtylopteryx hebardii Rehn 1905

The holotype and allotype (from Carrillo, Costa Rica) were remeasured, and supplemented with a sample of 10 males and 10 females from nearby Puerto Viejo de Sarapiquí, 25 km distant. The dimensions of the types fell within the range of the modern sample. The two were combined, and this sample is referred to as *M. hebardii* s.str. The normalized dimensions of a sample of 7 further males and females from higher localities in the Northern Cordillera all fall within the range of the former sample, except that the breadth of the fastigium is uniformly slightly (3%) greater (see Appendix 3 for the males' data). The two samples were therefore combined as *M. hebardii* s.l. This provides a basis for comparison with the other described taxa of this subgenus.

Microtylopteryx hebardii caligo Rehn 1955

This taxon is based on 2 males and a female from La Palma, Costa Rica, at approximately 1500 m altitude. The little remaining woodland at this locality is now very degraded, and new specimens could not be obtained.

The female allotype was found to be extensively damaged, but clearly a late instar larva, and probably recently moulted. It therefore cannot be compared with the *hebardi* s.l. sample discussed above. The raw dimensions of the two males all lie completely within the range of the larger male sample or largely overlap it; the normalized measures and shape ratios all lie within the confidence limits of the larger sample, except for the width across the genae and the length of Ta3, both of which are slightly (1 to 4%) smaller than recorded in the larger sample.

Rehn's (1955) diagnosis attributed to *M. h. caligo* the following characteristics: eyes less protuberant, head broader across the genae, hind metatarsus longer. None of these are supported by measurement. He also pointed out that the fastigium of *caligo* was more downwardly sloping than in *M. h. hebardii* and the fastigiofacial angle more broadly rounded (these are two ways of saying the same thing). This is true, though the effect is small (see Fig. 2). Alone, however, it seems to be an inadequate basis for subspecific rank, especially in the absence of a larger sample demonstrating that it is indeed a characteristic of a population.

In the absence of a difference between *M. h. hebardii* and *M. h. caligo*, the two sets of measurements were pooled and used to compare with the next taxon.

Microtylopteryx nigrigena Hebard 1924

Only 3 males were available, including the type and paratype (the taxon is rare). They are smaller than *hebardi*, by, e.g., 5% on average in the case of P; 27 of the 45 individual measurements made, fall beneath the *hebardi* range. After normalizing, however, the number of outliers falls to 14 out of 45, and these are diffusely scattered over 10 different characters. There is one exception—the hind femur F is smaller in all 3 males, by 17% on average.

In the females (N=4) most raw dimensions overlap those of *hebardi*, but their lower extremes fall below the limits of the latter species in 10 of the 15 measures; in the case of F and G-G, all 4 individuals are below the *hebardi* limits. After normalizing, however, all values, including F, are within the limits of *hebardi*, except for a

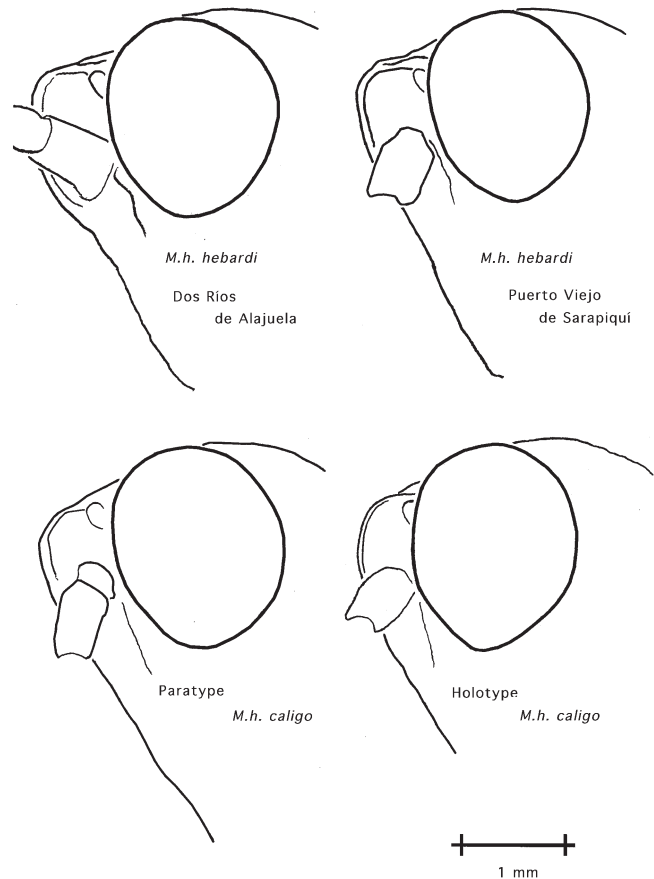


Fig. 2. *Microtylopteryx hebardii*. Comparison of profiles of heads of males of *M. h. hebardii* (sensu Rehn) and *M. h. caligo* Rehn.

single individual in which Fastigium L/P (and thus Fastigium L/B) is slightly smaller, and another in which Ta2/P is.

Rehn (1929) wrote that *nigrigena* is smaller than *hebardi*, as also shown here, and that the limbs are shorter, which is weakly supported by the above result on the hind femur of males only. He also claimed that the head is narrower; this is not confirmed by measurement, as all relevant normalized measures (E-E/P, IOS/P, G-G/P, E-E/G-G) are the same. Hebard (1924) thought the fastigium was shorter than in *hebardi*, but the normalized values overlap almost completely (0.13 to 0.16P in *nigrigena*, 0.14 to 0.17P in *hebardi*).

The only remaining differences between the two taxa are in color, and these are quite large; in *nigrigena* the face of the male is uniformly dark brown, not yellow in the lower half; the paler markings tend to white rather than yellow; the leading (ventral) edge of the tegmen is pale, not dark; and the proximal part of the ventral outer surface of the hind tibia is blueish rather than dark green. *M. nigrigena* is further apparently confined to Central Panama, where *M. hebardii* is absent. These seem appropriate differences for a subspecific rather than a specific rank.

Subgenus *Tristanacris*

A. Internal and external genitalia.— These were examined in all the populations discussed below. Within this subgenus no significant differences in genitalia were found. The genitalia are illustrated in the taxonomic section below.

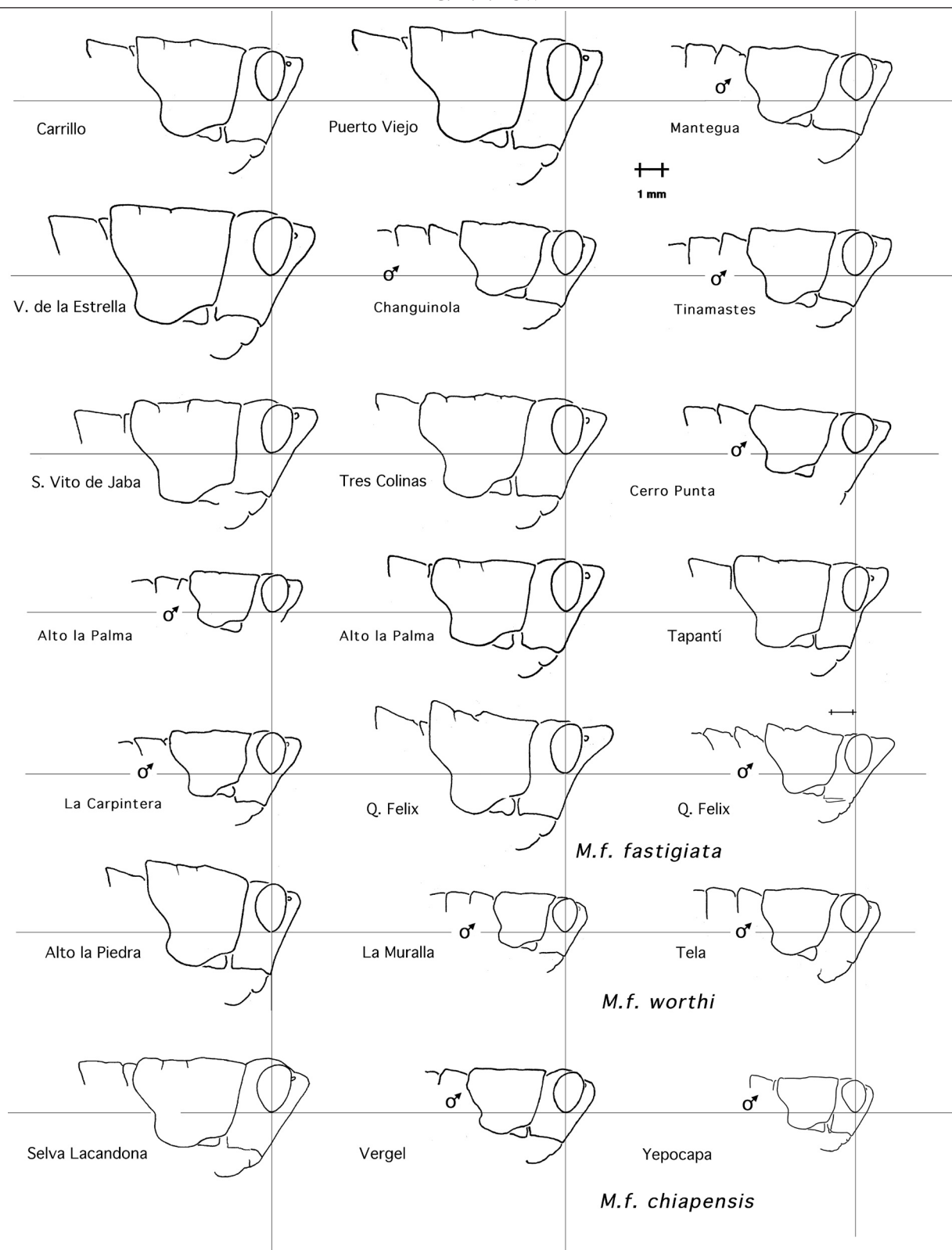


Fig. 3. Lateral profiles of head, pronotum and first abdominal tergum in various populations of *M. fusiformis*, to show the variation in size, shape and degree of fastigial elongation. Specimens are female unless otherwise indicated. The 3 pairs at the bottom right are *M. f. fastigiata*, *M.f. worthi* and *M.f. chiapensis* respectively; the remainder are all *M. f. fusiformis*. The top row corresponds to *M. f. fusiformis sensu* Rehn; Valle de la Estrella is the type locality of *M. talamancae* Rehn, and Changuinola is the Panamanian locality closest to the V. de la Estrella; Tinamastes, Tres Colinas, and S. Vito are localities in S.W. Costa Rica, the last close to the Panamanian Cerro Punta; La Carpintera, Alto La Palma and Tapantí are localities for *M. tristani* Rehn; Alto La Piedra, Panama, is the most south-easterly extreme of the currently known distribution, and Selva Lacandona, Mexico, appears to be the most northerly extreme of *M.f. fusiformis*.

B. Morphometry.—This taxon displays a bewildering variety of minor differences in size and shape - see Figs 3 and 4 for examples of the variation in fastigium and pronotal profile. Statistical morphometrics are strongly indicated.

Costa Rican populations

1. *M. fusiformis* Rehn 1905

a. The type (lowland) population

Rehn (1905) reported that his original type series consisted of 4 males and 3 females. However, in the collections of the ANSP there are 5 males and 9 females (one of which is larval) which bear his holotype, allotype or paratype labels. Twelve of these came from Carrillo and 3 from Guápiles, the latter being 1923 specimens used as the type series of *M. fusiformis fusiformis* Rehn 1929; the two localities are only about 15 km apart, at the northern foot of the escarpment of Costa Rica's Cordillera Central, at around 350 m altitude. These specimens were measured.

The type series was supplemented with insects collected recently from the same area and from the nearby lower Sarapiquí valley

(about 25 km away, localities between 45 and 700 m). A sample of 10 males and 8 females was measured, and the type series compared with this. The small size of Rehn's sample of males makes a formal comparison of the means problematic; a t-test (though with only 12 degrees of freedom) gives no significant differences, and virtually all the values of all Rehn's specimens fall within the 95% confidence limits of the modern sample. There were no significant differences between the means of the females, except that the fastigium is on average 3% narrower in the modern population ($P \approx 5\%$). The two samples were therefore combined.

b. Cordillera del Norte populations

A further sample of specimens (10 males, 8 females) was taken from localities in the Cordillera del Norte (Monteverde, Volcán Tenorio, V. Rincón de la Vieja and V. Cacao), all from higher altitude (around 1100 m) than the previous sample. Until very recently these populations must have been confluent with each other and with the lowland population considered above. The only significant difference in means shown by the males of this Cordillera population is a slightly larger foot (0.34P instead of 0.30P) but the ranges of individual values of this character overlap and it does not discriminate individuals of the two populations.

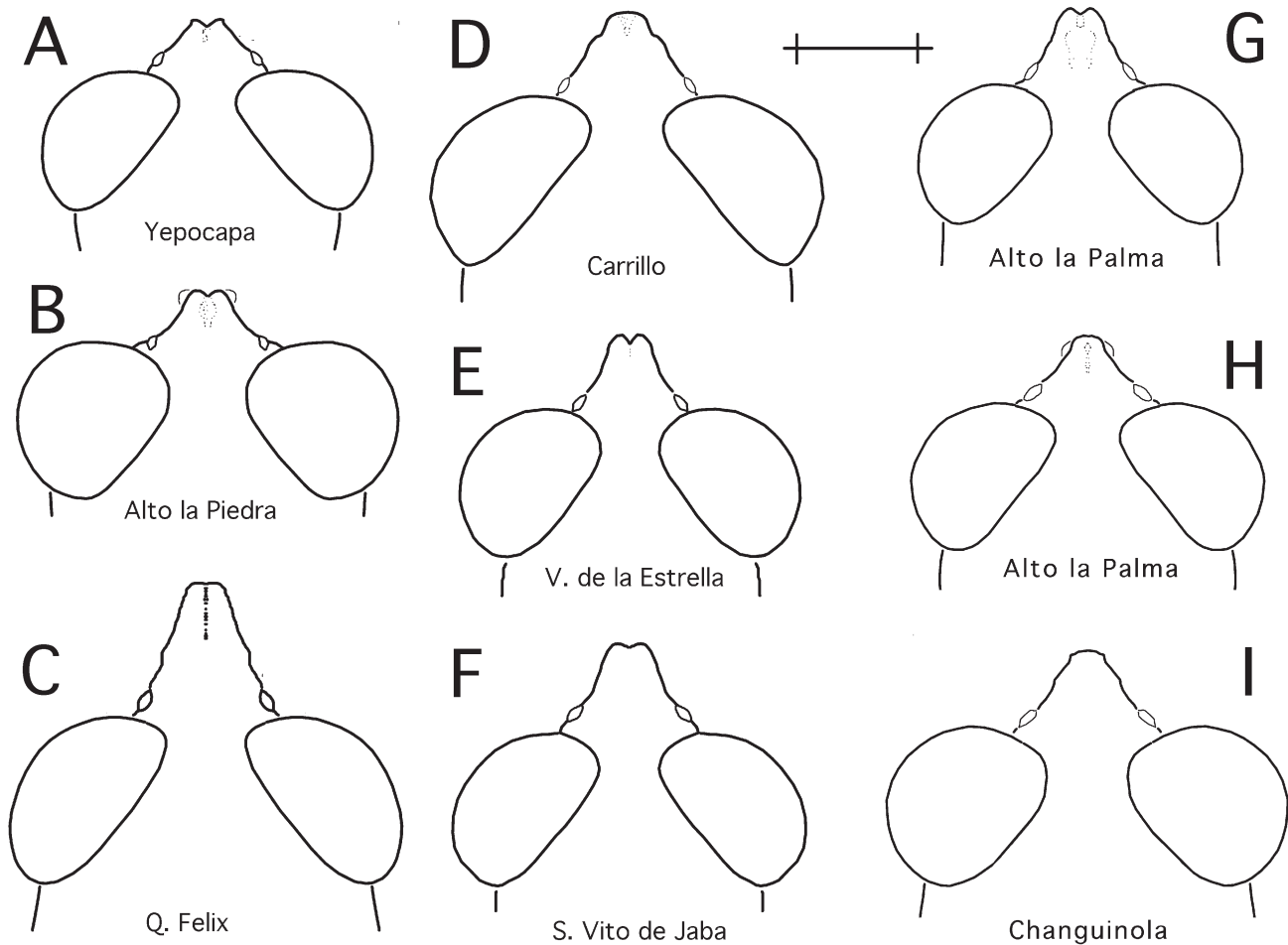


Fig. 4. Dorsal profiles of the head in various populations of *M. fusiformis*, to show the variation in size, shape, and degree of fastigial elongation. Specimens are all male. A. *M. f. chiapensis*, Guatemala. C. *M. f. fastigiata* n. ssp, Panama. (*M. f. worthi*, Honduras, is shown in Fig. 5). The remainder (B, D-I) are all *M. f. fusiformis*. Carrillo is the type locality; V. del la Estrella is the type locality of *M. talamancae* Rehn; Alto la Palma is the type locality of *M. tristani* Rehn. Note the differences between the 2 specimens from Alto la Palma, G & H. Differences of this order are found in all localities. Scale bar: 1mm.

The females of the Cordillera population show several small differences from the lowland one:

- Raw data: the distance across the eyes is significantly less, and there is a suggestion ($P \approx 5\%$) of a longer fastigium, a narrower femur and shorter tegmen.

- Normalized data: only the longer fastigium survives as a possibly significant difference.

- Shape ratios: the fastigium is significantly more gracile (*i.e.*, $F L/B$ is greater), and possibly ($P \approx 5\%$) the eyes are less protuberant ($E-E/G-G$).

The two populations, however, overlap extensively in all of the above characters, none of which discriminates reliably between the populations. This population was therefore combined with the previous one to give the population Northern Costa Rica *M. fusiformis* ($N_{\text{female}} = 24$; $N_{\text{male}} = 25$).

2. *M. fusiformis lamprus* Rehn 1929

Rehn described this subspecies on the basis of 2 individuals, one of which he described as "atypical". To these were added a recent specimen from Hacienda Tiquirres, a relict woodland close to the original type locality (which is otherwise largely under cultivation or denuded nowadays). No females are known from that area.

Forty-two of the 45 measurements made on these 3 individuals fall within the 95% confidence limits of the Northern Costa Rica *M. fusiformis* male sample, as do 56 of the 60 calculated ratios. Rehn's diagnosis claims that the eyes are less protuberant in *lamprus*, but the ratio $E-E/G-G$ in his *lamprus* specimens is 1.08 and 1.22, compared with the *f. fusiformis* sample mean of 1.14 ± 0.04 , so even the most extreme *lamprus* specimen lies well within the 95% limits for *fusiformis*. He also stated that the profile of the frons is straight, rather than concave. This is a function of the length of the fastigium, which is variable; the longer the fastigium, the more concave the profile. In the holotype the fastigium length is 0.20P, compared with a range of 0.16 to 0.23P in the *f. fusiformis* sample. Finally, Rehn implies that the fastigial lateral margins are not concave in *f. lamprus*, whereas he says that they are concave in *f. fusiformis*. Among the Northern Costa Rica sample of *fusiformis* there are 18 individuals with concave fastigia and 4 with straight ones; of the *lamprus* specimens, the holotype has straight sides, the paratype slightly concave, and the new specimen from Hacienda Tiquirres has concave ones. There seems no justification to split a subspecies *f. lamprus* from *f. fusiformis*.

3. *M. talamancae* Rehn 1929

Rehn's extensive type series, comprising 19 males and 18 females, all came from the lowland Valle de la Estrella, on the east side of the Talamanca range. Of these, 22 have been traced in the ANSP, and 10 of each sex remeasured. In addition, a modern sample of 10 males and 2 females from that region was measured. The 2 samples of males show no significant differences in any measurement or ratio; the insects in Rehn's sample are slightly but not significantly larger on average (for the dimension P, for example, by 5%). All values for the 2 modern females lie within the 95% confidence limits of Rehn's sample. The two samples were therefore combined to represent the Estrella population, with $N_{\text{male}} = 20$ and $N_{\text{female}} = 12$.

The averages of this Estrella population show several significant differences from those of the Northern Costa Rica *M. fusiformis* sample.

Males

- Raw measurements: both the 2nd tarsal segment and the tegmen are shorter.

- Normalized measurements: as above, and also the femur is significantly shorter (2.51P as opposed to 2.62P, a difference of 4%).

- Shape ratios: fastigium length/breadth is larger (0.65 as opposed to 0.61) and this is weakly significant ($P \approx 3\%$). (This fact shows the virtue of calculating the ratio $\text{Fast } L/B$ – the normalized fastigium length alone is not greater than that of *fusiformis s. str.*, nor is the fastigium breadth significantly smaller).

- The median number of internal spines on the hind leg is 9 rather than 8.

In females, the only weakly significant difference ($P \approx 5\%$) between the two populations is the longer fastigium and hence the larger ratio fastigium L/B of the Estrella population (0.7 as opposed to 0.65).

Rehn (1929) noted that the Estrella population had a longer and/or more slender fastigium, but did not record any difference in the other characters. He claimed that the head was narrower than in *fusiformis*, but the statistics show that this is not so; his eye was probably deceived by the longer fastigium. He also claimed that the medial carina is less arcuate and that the male cerci are more recurved dorsally, but I cannot confirm this.

In all cases, however, the range of values found in the Estrella population overlaps that found in the *fusiformis s. str.* population, and no character can be used to determine whether a given individual belongs to one or the other population. These slight though significant differences between the two populations do not therefore seem sufficient to warrant a specific or even a subspecific distinction.

4. *M. tristani* Rehn

The type series came from 3 different localities, all at relatively high altitude around the rim of the Meseta Central: Alto la Palma, on the saddle between V. Barba and V. Irazu; Cerro Candelaria, above Tres Ríos; and Navarro, in the upper basin of the Río Reventazón. The 7 males of the type series were measured. A further 10 males collected recently from Alto la Palma, from Cerro Candelaria and from Orosi and Tapantí, near Navarro, were also measured. There were no significant differences between this sample and the type series, so the 2 samples were combined. A sample of 10 females, including 7 of the type series, was also measured.

The combined samples ($N_{\text{males}} = 17$, $N_{\text{female}} = 10$) were then compared with those of northern *fusiformis*. In males the results were as follows.

- Raw dimensions: all dimensions are significantly smaller on average in *tristani*, except the length of fastigium. Note, however, that the ranges of all dimensions overlap – there is none that discriminates between the two populations.

- Normalized dimensions: in *tristani*, the antennae are significantly shorter and the IOS is narrower than in *fusiformis*. The fastigium may possibly ($P = 5\%$) be narrower, and is certainly very significantly longer, and the head is taller (C-V), probably because of having more carina on the vertex. The hind femora are possibly ($P = 5\%$) more slender. The tegmina are slightly longer, but not significantly so. Note again that all normalized dimensions overlap between the two taxa – there is no normalized dimension that discriminates between the two.

— Shape ratios: the hind femur is significantly more gracile (*i.e.*, F/FD is greater). The fastigium is longer and the head is taller (C-V/G-G). The shape ratios too, all overlap, there is no single discriminating ratio.

— The median number of internal spines on the hind leg is 9 rather than 8.

In females, the position is similar. All raw dimensions of *tristani* are smaller, most of them significantly so. In contrast, in the normalized values, only the longer fastigium and (unlike the males) the longer tegmen of female *tristani*, are clearly significantly different. There is no difference in antennal length or interocular space, and the higher head and more slender femur are only doubtfully significant, as in the male. The median number of internal hind tibial spines is again 9.

Most of these differences were correctly described by Rehn in 1929 (see Appendix 1). Again, they do not seem to merit a specific distinction, as all of them are statistical, and the ranges overlap; no single character or combination of characters discriminates individuals reliably. This is biologically reasonable, as there is continuous woodland and presumably a continuous *fusiformis* population stretching from Alto la Palma (the type locality of *tristani*) to Carrillo (the type locality for *fusiformis*), down the valley of the Río Hondura. The specimens from Candelaria and Navarro localities, which are intermediate in altitude between Alto La Palma and Carrillo (though not in their proximity), are indeed also intermediate in size.

5. South-Western Costa Rica

A major area of Costa Rica containing *Tristanacris*, which was not sampled by Rehn, consists of midelevations on the Western side of the Talamancas, stretching from the upper Valle de El General to the Panamanian border. A sample of 11 males and 5 females from various localities within this region was measured.

When compared with the northern Costa Rica *fusiformis* population, the males of this southwestern population (like the Estrella population) differ only in having a slightly but significantly slimmer hind femur, and a tendency to more internal spines on the hind tibia (median 9 rather than 8). There is a weak suggestion ($P = 5\%$) of a possibly broader and longer fastigium and a taller head. The female sample is too small for a comparison of means; when compared with the 95% confidence limits of the northern *fusiformis* sample, only 5 of 100 normalized values lie outside of the limits.

The ranges of all these characters however overlap very strongly those of the *fusiformis s.str.* population, providing no discrimination. (The Estrella population differs from the southwestern population in the same characters as it does from *fusiformis s.str.*, *i.e.*, in having a narrower fastigium, a shorter second tarsal segment, and a shorter tegmen).

Summary of results of analysis of Costa Rican populations

In view of the above analysis I see no evidence for the existence of more than one taxon (*M. fusiformis* Rehn 1905) of the subgenus *Tristanacris* in Costa Rica. The means, range and standard deviations for all characters were therefore recalculated using the combined data ($N_{\text{males}} = 79$, $N_{\text{females}} = 51$). This is referred to in the next section as the Costa Rican *fusiformis* sample.

Panamanian populations

In Panama, *M. (Tristanacris)* is known so far only from the Western part of the country. Three populations there have been sampled in numbers large enough to permit statistical comparison with the Costa Rican sample.

6. Río Changuinola

A large series of *Tristanacris* was collected in the United Fruit farms of this area by F. W. Walker in 1923, in the Caribbean coastal area of Prov. Bocas del Toro, near the Costa Rican frontier.

A series of 10 Changuinola males and 10 females were measured, and the results compared with the summed Costa Rican population. Males show the following differences.

— Raw data: the only statistically significant differences are a shorter fastigium and a shorter Ta2 in the Changuinola population. The ranges however overlap.

— Normalized data: the Changuinola population has a significantly shorter fastigium, and shorter Ta1 and 2; there is also a suggestion of a shorter femur and lower head. All ranges, however, overlap.

— Shape ratios: in the Changuinola population Fast L/B is significantly smaller, and it has significantly short femora, and slightly but significantly more protuberant eyes — this last character was unexpected, as neither G-G nor E-E were significantly different on average. All ranges overlap.

Females are similar:

— Raw data: the Changuinola females have a significantly shorter fastigium (and possibly a broader one too) and shorter Ta2. The ranges overlap.

— Normalized data: significantly shorter fastigium, significantly smaller (lower and narrower) head, and all tarsal measurements are either significantly smaller or approaching this condition.

— Shape ratios: significantly squatter fastigium and more prominent eyes (here clearly a consequence of the narrower head), and perhaps a shorter femur.

All the above characters overlap in range with the Costa Rican sample; no measures are discriminant.

When the Changuinola population is compared with the Estrella population, the geographically nearest large sample, most of the trends listed above are still present. The differences and t-values are however smaller, and the differences in head height (C-V), femur length, Ta1, and foot length disappear in the normalized values. These circumstances show that the Estrella and Changuinola populations share many of the same trends. The shorter fastigium and more protuberant eyes of the Changuinola sample, however, persist in both comparisons and their t-values increase in the comparison with the Estrella population, though the ranges still overlap. These two characters are thus Changuinola specialities.

A small recent sample (3 males and 2 females) was available from the village of Wekso, on the Río Teribé, a tributary of the Río Changuinola. It does not appear to differ from the Changuinola population.

The differences shown by this population do not allow individuals belonging to it to be unambiguously separated from the Costa Rican population.

7. The Alto la Piedra population

A second Panamanian population from the continental divide in Veraguas Province has been studied. Eight males and 6 females were measured and the results compared with the combined Costa Rican population.

Males

— Raw data: mostly no significant differences, but the head measurements are wider (possibly significant), the femur larger (broader and longer - both possibly significant), and antennae and fastigium are both significantly shorter.

— Normalized dimensions: significantly shorter antennae and shorter fastigium, maybe a thicker femur and shorter foot - but all these overlap completely in range with the Costa Rican population.

— Shape ratios: a significantly shorter foot and fastigium, and maybe a heavier femur (*i.e.*, F/FD is larger) — but once again there are high degrees of overlap.

Females

The number of females is too small for a t-test. The individual measurements were compared with the confidence limits for the Costa Rican sample.

— Raw data: all individual values lie within the 95% confidence limits of the Costa Rican population.

— Normalized data: all values lie within the 95% confidence limits of the Costa Rican population, except single values of L/P and Ant/P, which are below the range of the Costa Rican sample.

— Shape ratios: all individual values lie within the 95% confidence limits of the Costa Rican population.

The differences shown by this population do not allow individuals belonging to it to be unambiguously separated from the Costa Rican population.

8. The Cerro Punta population

A single male specimen and three females were available from Cerro Punta, on the Pacific side of the watershed close to the border with Costa Rica. Dimensions and proportions correspond closely (as might be expected) with the SW Costa Rican population of *fusiformis*. All the measured values lie within the 95% confidence limits of that population.

9. The Bocas del Toro Highland population

The individuals measured all come from the highlands of Provincia Bocas del Toro, Panama, from the continental divide at around 1000 m down to 800 m on the Caribbean slope. (There is also one museum specimen labelled as coming from Ciudad Bocas del Toro, at sea level on Isla Colón, which is indistinguishable from them. This may, however, be a mistake in labelling, especially as another specimen from Isla Colón is similar to the Changuinola sample.) A sample of 8 males and 5 females was compared with the combined Costa Rican sample.

Males

— Raw data: all dimensions except tegmen and tarsal measurements are larger, 8 of the 15 significantly so (mean of P is 1.13× larger). In all but one character there is however marked overlap with the Costa Rican population. The exception: the raw fastigial

length is very significantly larger and there is no overlap (range, combined *fusiformis* sample, 0.45 to 0.86 mm; range, Bocas sample, 0.96 to 1.12 mm).

— Normalized dimensions: all head measurements (C-V, IOS, E-E, G-G, and Fast B) are smaller, mostly significantly so. The fastigium is highly significantly longer. The tegmen, and Ta1 and Ta2 are significantly shorter. All these measures overlap the larger sample, except fastigium length, which shows almost no overlap with the Costa Rican population.

— Shape ratios: fastigium is much longer and relatively narrower, highly significantly so, and with no overlap (mean Fast L/B = 0.95, versus 0.65). The head is also significantly more compressed laterally (C-V/G-G). There is no change in the ratio foot/femur; although the foot is slightly shorter, so is the femur, and so the ratio does not change. Additionally, the dorsal profile of the pronotum and first 2 abdominal segments is noticeably more jagged than in other populations (see Fig. 3).

Females

— Raw data: for all 5 females, 11 of the 15 measures fall completely within the limits of the combined Costa Rican and Panama female sample, while 3 (Ta3, antenna, and overall length) largely overlap. As in the males, the length of fastigium shows no overlap, it is clearly longer than in the other sample (Fast L = 1.24 to 1.51 mm versus 0.67 to 1.15 mm).

— Normalized data: thirteen of the 15 normalized measures fall completely within the larger sample, and one (Ta3/P) overlaps it. The normalized fastigial length (Fast L/P) shows effectively no overlap (0.25 to 0.32 versus 0.14 to 0.25).

— Shape ratios: three of the 5 shape ratios fall completely within the confidence limits of the larger sample, and one overlaps it. Fastigium L/B shows no overlap at all (0.91 to 1.06 versus 0.46 to 0.84).

This population thus has a nonoverlapping character allowing all individuals of both sexes to be discriminated from the remainder of the *Tristanacris* populations. As such it seems to warrant subspecific rank, and is described as *M. f. fastigiata* below.

Summary of the Panamanian populations

In none of the above Panamanian populations, other than the Bocas del Toro Highland population, can a randomly chosen individual be discriminated from the Costa Rican sample, although each has statistically significant characters at the population level. In the absence of discriminating characters, these other Panamanian populations were added to the Costa Rican ones and the means and standard deviations calculated for the entire sample. In subsequent comparisons this combined sample is referred to as *M. fusiformis*, with no further qualification.

Northern Central American populations

NICARAGUA

A single male from Matagalpa falls completely within the range of values for *fusiformis* from Costa Rica and Panama, and is very close to their average in all characters.

HONDURAS.

10. *M. worthi* Rehn 1955

The type series, from Lancetilla, near Tela, at sea level on the Caribbean coast of Northern Honduras, consists of 2 males and 2 females. These were supplemented with a further 7 males and 4 females from Tela itself, about 5 km from the original type locality, and all were measured and compared with the *fusiformis* s.l. sample.

— Raw data: there are numerous, probably significant, differences between the averages for the 2 populations; *M. worthi* has on average longer antennae, wider eyes, a very short fastigium, a higher head capsule, longer femora, a very short tegmen, and possibly longer hind tarsal segments and foot. (Contrary to Rehn's description, the interocular space is not significantly different from that of *fusiformis*). For most of these characters, however, the ranges overlap largely or completely. There are however 3 exceptions: the very short tegmen of *worthi* — at its longest only about 70% the length of the shortest record for *fusiformis* — is completely distinct, and the very short fastigium shows almost no overlap with the *fusiformis* range of values.

— Normalized data: these show much the same differences as the raw data. Both tegmen and fastigium are very significantly shorter than in *fusiformis*, and show either little overlap or none at all.

— Shape ratios: the femoral proportions are slightly longer and slimmer, but the range overlaps completely with that of *fusiformis*. There is no difference between the 2 populations in ratio of foot/femur — both values are slightly larger in *worthi*, so the ratio remains unchanged. The eyes are significantly more protuberant on average, but the ranges overlap very largely.

Only 6 females were available. Their individual measurements were compared with the 95% limits for *fusiformis* (Panama and Costa Rica).

— Raw data: the short tegmen of all individuals falls outside the *fusiformis* limits. Of the remaining 83 individual measures, only 1 falls outside these limits.

— Normalized data: tegmen and fastigium are shorter in all individuals. Of the remaining 76 measurements, only 2 fall outside the *fusiformis* range (a longer antennal flagellum and a longer body).

— Shape ratios: in 5 of the 6 individuals, the ratio fastigium L/B is shorter than the lower limit for *fusiformis*.

[It may be remarked here that Rehn's (1955) published measurements of the type series of *worthi* are unusually inaccurate, being uniformly too large, by up to 10%. His paper gives the impression that *worthi* is a larger species than *fusiformis*, but there is in fact no significant difference in either P or L. F is significantly longer on average in *worthi*, but the ranges overlap almost completely.]

The status of *M. worthi* is not, however, as clear as the above would suggest.

a) The tegmen (Fig. 5): A further small sample of individuals from other regions of Northern Honduras was available, and these all lack the short tegmen of *M. worthi sensu* Rehn. (Some of these are from Progreso, about 60 km WSW of Tela, and somewhat higher, at around 200 to 300 m. Two more are from La Muralla, about 130 km ESE of Progreso, and still higher, at around 1000 m. Both localities are on the Caribbean slope, about 50 and 80 km from the sea respectively. See map, Fig. 10C). The 5 available males were measured and compared with both the *fusiformis* and the *worthi* populations. They show no differences at all from *worthi*, other

than in the length of the tegmen, but numerous possibly significant differences from *fusiformis*. It is clear that all the Honduran specimens belong to the same taxon. The simplest explanations of these findings are that either *M. worthi* is genetically polymorphic for wing length, or (more probably) that it exists in local races, of which only the Tela population has the short tegmen.

b) The fastigium (Fig. 5): when the males of the Honduran populations were combined (thus giving a more reasonably sized sample, N = 14) as *M. worthi* s.l., and their means and standard deviations compared with those for *fusiformis*, the two taxa are found to be significantly different in many respects (see Appendix 2). Unfortunately, in virtually all characters the ranges overlap, often completely. The only characters which show the potential of discriminating all individuals of *worthi* s.l. from those of *fusiformis* are the normalized length of the fastigium, Fast L/P, and the related aspect ratio of the fastigium, Fast L/B. The former ranges from 0.10 to 0.15 in *worthi* s.l. and from 0.13 to 0.25 in *fusiformis*, and the latter ranges from 0.36 to 0.46 in *worthi* s.l. and from 0.44 to 0.84 in *fusiformis*.

The fastigium of *worthi*, however, is almost indistinguishable from that of the *fusiformis* population from Alto la Piedra, Panama, (Fig. 4B) which also has very short fastigia. The two populations can be readily distinguished by the much longer antennae of *worthi* (1.82 to 2.30P versus 1.19 to 1.34P in males, 1.31 to 1.45P versus 0.81 to 0.93P in females) and the longer hind femora (2.54 to 2.97P versus 2.49 to 2.66P in males, 2.42 to 2.55 versus 2.26 to 2.42 in females) — but these characters do not differentiate *worthi* from other *fusiformis* populations.

This analysis leaves *M. worthi* s.l. in the invidious position of being clearly defined (i.e., by tegmen length) in one morph or population, but only by a combination of ratios (Fast L/P, F/P, Ant/P) requiring accurate measurements under a microscope in the other. This is obviously too slender a basis for a specific distinction, especially considering the lack of all genitalic differentiation. I therefore propose to reduce the taxon to subspecific rank.

GUATEMALA

11. The Yepocapa and Vicinity population

A sample of 9 females and 9 males was available from Yepocapa and vicinity, on the Pacific slope of the Western volcanic chain near Antigua. These individuals are notable for their small size (mean length of male 11.58 mm), smaller than *M. chiapensis*, to which they are otherwise similar.

In the male all raw dimensions, other than antennae and tarsal segments, are significantly smaller than in *fusiformis*.

After normalizing, most dimensions are still significantly different from *fusiformis*, the exceptions being the length of the tegmen and width of the interocular space. This population has on average a significantly longer body and antennal flagellum, wider eyes, a shorter and broader fastigium, a larger head, longer and broader femora, and longer tarsi; there is no overlap between the 2 populations in the normalized length of the femur.

The shape ratios indicate a more gracile femur and a shorter and broader fastigium. The eyes may be (P ca 0.05) slightly more protuberant.

In the female, all raw dimensions are smaller than in *fusiformis*, and all are significantly so, except the antenna; the fastigium is much shorter and does not overlap the *fusiformis* range.

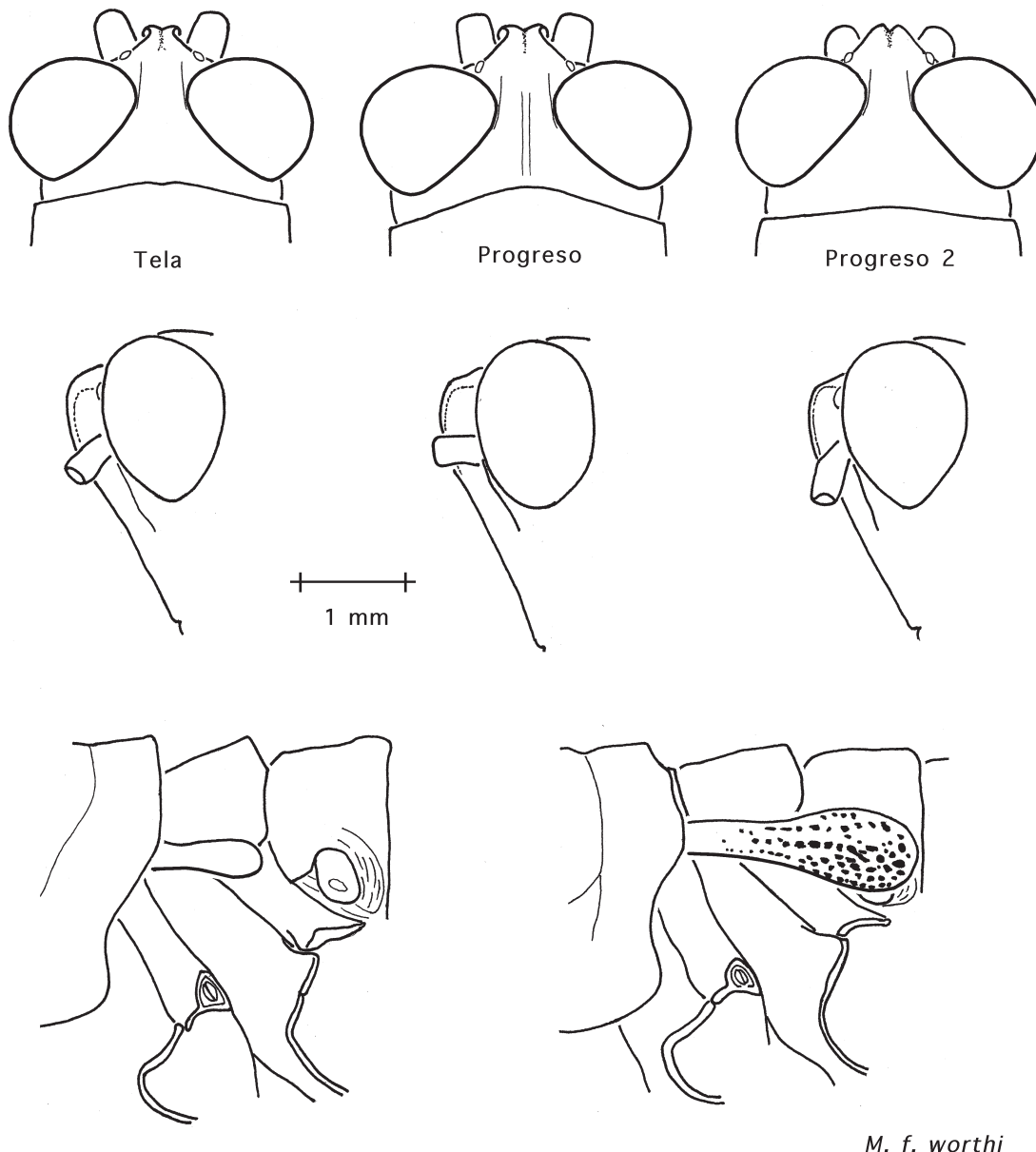


Fig 5. *M. fusiformis worthi*. Comparison of male fastigia in dorsal view (top row) and lateral view (2nd row), and of male tegmina (3rd row). In all cases the left-hand specimen is from the type locality at Tela, and the center and right specimens are from El Progreso. Note that while most Progreso specimens have the typical broadly grooved, concave-sided fastigium also seen at Tela, some ("Progreso 2") have a straight-sided fastigium with a narrow apical groove, a shape commonly seen in other populations of *fusiformis*. This is thus only a probabilistic character for *f. worthi*. In side view, however, the two are not different (second row). The Tela population, but not others in Northern Honduras, has reduced tegmina (bottom row).

MEXICO

After normalizing, only the tegmen and the interocular space are not significantly different. The population is relatively longer, has longer antennae and is wider across the eyes, has a shorter and wider fastigium, a longer and wider femur, and larger head and foot than does *fusiformis*; there is no overlap between the 2 populations in the relative length of the femur.

In the shape ratios, average Fast L/Fast B is very significantly smaller than in *fusiformis*, and the height of the head (C-V/G-G) and the protrusion of the eyes (E-E/G-G) are also significantly larger. All these values, however, overlap with the *fusiformis* range.

12. *M. chiapensis* Rehn 1955

This taxon is based on a single male holotype. A further male and a female from Chiapas were obtained from the Paris museum. These 3 individuals were compared with the Costa Rican and Panamanian *fusiformis* sample, the Honduran sample, and the Guatemalan sample from Yepocapa described in the preceding section.

The raw measurements of the 2 males all fall within the range shown by *fusiformis*, but there are differences in proportions. Of the 28 normalized measurements, 6 fall outside the *fusiformis* limits;

both specimens show a relatively larger femur and 1st tarsal segment. In the shape ratios, one of the Chiapas specimens has a short fastigial L/B ratio falling outside the *fusiformis* range. Examination of Rehn's diagnosis (Appendix 1) shows that he correctly identified the short fastigium and the longer femur (though he described it as more slender, rather than longer).

When compared with the Guatemalan sample, different results are obtained. The Chiapas males are larger than the Guatemalan ones in all dimensions, 18 of the 30 raw measurements falling above the Guatemalan upper 95% confidence limit. Strikingly, however, all of the normalized dimensions and all the shape ratios fall within the Guatemalan limits. These findings suggest that the Guatemalan population is a small race of *M. chiapensis*.

(The same does not however hold for the sole Mexican female known. This is not only larger than the Guatemalan population, but also 11 of its 15 normalized dimensions fall outside the confidence limits of the Guatemalan sample. By contrast, all its parameters fall within the *fusiformis* confidence limits. This suggests that it is not *chiapensis*, and that *fusiformis* extends as far as SE Mexico. All true *chiapensis* known from Mexico and Guatemala are from the Pacific slope, whereas this Mexican female is from the Selva Lacandona, draining into the R. Usumacinta and the Caribbean).

M. chiapensis continues the trends already seen in the transition from *M. fusiformis* to *M. worthi* - reduction in fastigial length, longer and more gracile hind femora, and longer antennal flagellum. Indeed the range of the normalized femur lengths in males overlaps those in *worthi*. The question therefore arises as to whether *chiapensis* and *worthi* are in fact different. When the Guatemalan population is compared with *worthi* s.l., numerous significant differences in normalized values emerge: the former has broader eyes, broader and longer fastigium, a larger head, longer and broader femur, longer tarsal segments and foot, and perhaps a more elongate fastigium. All these values however overlap heavily in range, except fastigium length, where there is almost complete separation (Fast L/P = 0.14 to 0.17 in *chiapensis*, 0.10 to 0.15 in *worthi*).

M. chiapensis s.l. (i.e., the Guatemalan and the male Mexican specimens) can thus be distinguished reliably from *M. fusiformis* by the relatively longer femur, and from *M. worthi* by the longer fastigium, but shows no other discriminating characters. This is appropriate for subspecific rank.

II. Taxonomy

In view of the above analysis, the following revised divisions of the genus are proposed.

1. *M. hebardii* Rehn 1905.

M. hebardii hebardii Rehn 1929, new status.
= *M. fusiformis caligo* Rehn 1955, new syn.
(Range: Central Nicaragua to Northern and Eastern Costa Rica).

M. hebardii nigrigena (Hebard 1924), new status
(Range: Central Panama).

2. *M. fusiformis* Rehn 1905.

Microtylopteryx fusiformis fusiformis Rehn 1929, new status.
= *M. fusiformis lamprus* Rehn 1929, new syn.
= *M. tristani* Rehn 1929, new syn.
= *M. talamancae* Rehn 1929, new syn.
(Range: Western Panama to Central Nicaragua, possibly beyond).

Microtylopteryx fusiformis worthi Rehn 1955, new status.
(Range: Caribbean slope of Northern Honduras).

Microtylopteryx fusiformis chiapensis Rehn 1955, new status.
Range: Mexico (Chiapas), Guatemala.

Microtylopteryx fusiformis fastigiata new subspecies.
(Range: Caribbean highlands of extreme Western Panama).

As both the subgenera *Microtylopteryx* (*Microtylopteryx*) and *Microtylopteryx* (*Tristanacris*) proposed by Rehn (1959:113) are thus rendered monospecific, I consider them now redundant.

Redescriptions

Microtylopteryx Rehn 1905

Rehn 1905: 448

Type species.— *Microtylopteryx hebardii* Rehn 1905: 448.
Kirby 1910: 544.
Hebard 1924: 137.
Rehn 1929: 46.
Rehn 1955: 113.
Amédégato 1974: 202.

Etymology.— Greek *micros*, small; *tyle*, *tylos*, pad, knob, lump; *pteryx*, wing (feminine); "having wings like small pads".

Diagnosis.— (Figs 6-9) Small to medium-sized grasshoppers, adult body lengths 11 to 17 mm (male), 14 to 26 mm (female). Integument in general polished, pitted on thorax and head and dorsum of abdomen. Antennae filiform, the flagellum of 15 to 21 segments, segments 12 and 13 usually strikingly paler than rest. Fastigium short to moderately long, triangular, horizontal or downward sloping, often notched at anterior end by continuation of the groove of the frontal ridge. Face straight or slightly concave in profile. Frontal ridge well developed above medial ocellus, obsolete below, deeply grooved medially (Fig. 1), groove sometimes continued onto fastigium. Eyes globose; interocular space large, at least twice as wide as antennal scape (Fig. 1). Pronotum without lateral carinae but with well marked median carina. Posterior extremity of medial carina usually elevated into a prominent melanized tooth; metanotum, first and (to a lesser degree) succeeding terga of the abdomen, with similar, but usually smaller, teeth. Disc of pronotum crossed by two shallow sulci, which may or may not incise the medial carina. Anterior margin of pronotum convex, often emarginate in midline. Posterior margin of lateral lobe bisinuate. Prosternal process thin, vertical, sharply pointed. Brachypterous to micropterous; elytron extends maximally into 2nd abdominal segment. Hind femur with dorsal external face well developed, pitted, and colored a metallic gold; lateral external face smoothly polished, black with blue or green sheen. Dorsal medial carina of hind femur well developed, minutely serrate or granular in central region, terminating at the knee in small medial tooth. Lateral lobes of hind knee smoothly rounded. 6 to 7 external and 8 to 9 internal hind tibial spines, the most proximal in both rows often rudimentary.

Male furcula (Fig. 7) weakly developed, melanized. Supra-anal plate grooved medially in proximal region, triangular to oblong in outline, but terminating in a rounded tongue-like posterior process;

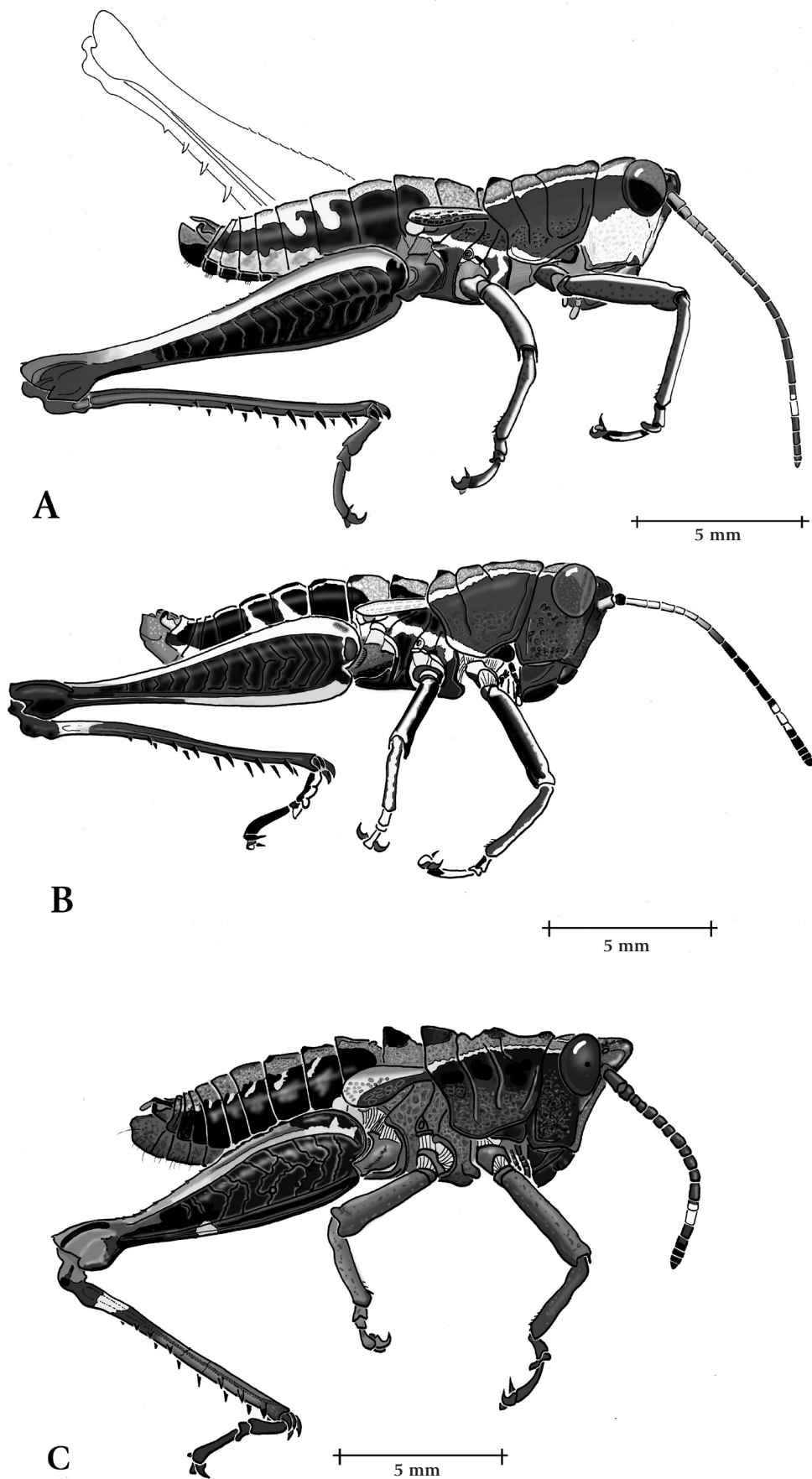


Fig. 6. Habitus pictures.
 A. *M. hebaridi hebaridi*.
 B. *M. hebaridi nigrigena*.
 C. *M. fusiformis fastigiata* n. ssp.
 Scale bars: 5 mm.

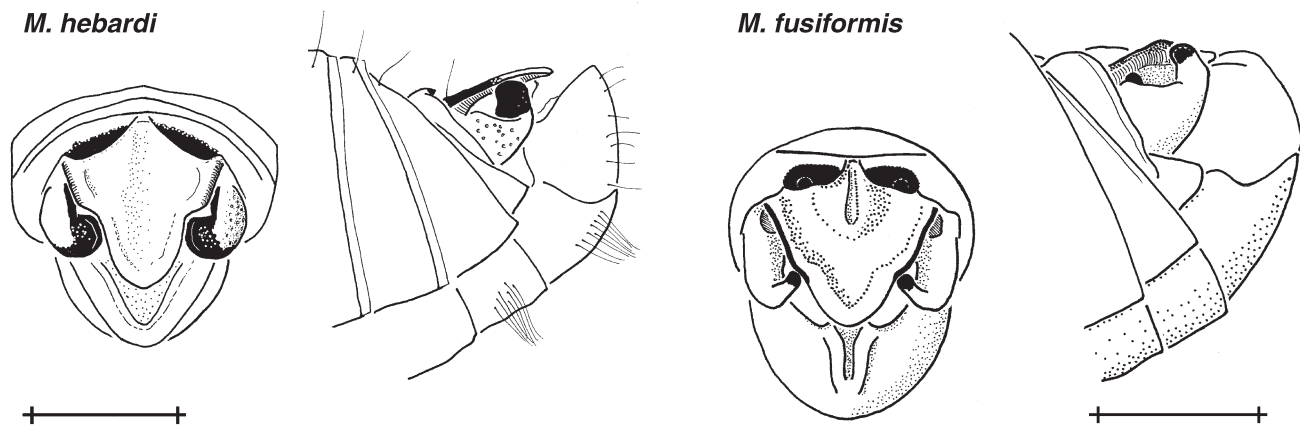


Fig. 7. External male genitalia of *M. hebardii* (left hand side) and *M. fusiformis* (right hand side). Scale bars: 1 mm.

Table 1. *Microtylopteryx* Rehn; dimensions in mm. Values are means \pm standard deviation, or (for small values of N) ranges.

<i>Microtylopteryx hebardii</i> Rehn								
Taxon	P		L		F		FD	
	Male	Female	Male	Female	Male	Female	Male	Female
<i>M. hebardii</i>	3.57 \pm 0.10	5.03 \pm 0.31	15.80 \pm 0.76	23.71 \pm 0.95	12.36 \pm 0.41	15.87 \pm 0.54	2.68 \pm 0.14	3.41 \pm 0.11
N	17	14	17	14	17	14	17	14
<i>M. h. nigrigena</i>	3.21 - 3.48	4.67 - 4.83	13.05 - 13.99	21.32 - 23.99	10.61 - 11.28	13.74 - 14.33	2.46 - 2.50	2.97 - 3.34
N	3	4	3	4	3	4	3	4
<i>Microtylopteryx fusiformis</i> Rehn								
Taxon	P		L		F		FD	
	Male	Female	Male	Female	Male	Female	Male	Female
<i>M. fusiformis</i>	3.42 \pm 0.27	4.64 \pm 0.33	13.54 \pm 1.03	19.44 \pm 1.46	8.81 \pm 0.63	11.38 \pm 0.70	2.57 \pm 0.24	3.31 \pm 0.24
N	100	69	100	69	100	69	100	69
<i>M. fusiformis chiapensis</i> *	3.02 - 3.08	unknown	12.65 - 12.93	unknown	8.65 - 8.82	unknown	2.29 - 2.46	unknown
N	2	0	2	0	2	0	2	0
<i>M. fusiformis chiapensis</i> **	2.73 \pm 0.11	3.61 \pm 0.15	11.58 \pm 0.32	15.78 \pm 0.64	8.29 \pm 0.16	10.19 \pm 0.48	2.20 \pm 0.09	2.71 \pm 0.13
N	9	9	9	9	9	9	9	9
<i>M. fusiformis worthi</i>	3.55 \pm 0.26	4.47 - 4.9	14.13 \pm 0.76	17.42 - 22.55	9.75 \pm 0.52	10.93 - 12.13	2.62 \pm 0.13	3.06 - 3.25
N	14	6	14	6	14	6	14	6
<i>M. fusiformis fastigiata</i>	3.70 - 4.13	4.74 - 5.23	14.20 - 15.76	20.77 - 22.54	9.53 - 10.33	11.76 - 12.48	2.63 - 2.89	3.15 - 3.49
N	8	5	8	5	8	5	8	5

* Mexican population

** Guatemalan population

Fig. 8. Internal male genitalia of *M. hebardii* (A-G) and *M. fusiformis* (H-N). Scale bars: 1 mm.

A: complete phallic complex, lateral view.

B: as A, but dorsal view.

C: as A, but with ectophallic membrane reflexed to show endophallus and cingular apodemes.

D: ectophallic membrane reflexed to show cingulum (black) and anterior endophallus, the arrow indicates a retractor apodeme*.

E: endophallus, arch (black) and superior aedeagal valves.

F: endophallus, ventral view; black, arch.

G: epiphallus, oblique posterior view.

H: complete phallic complex, lateral.

I: as H, but dorsal.

J: as H, but with ectophallic membrane cut away to show endophallus and cingular apodemes.

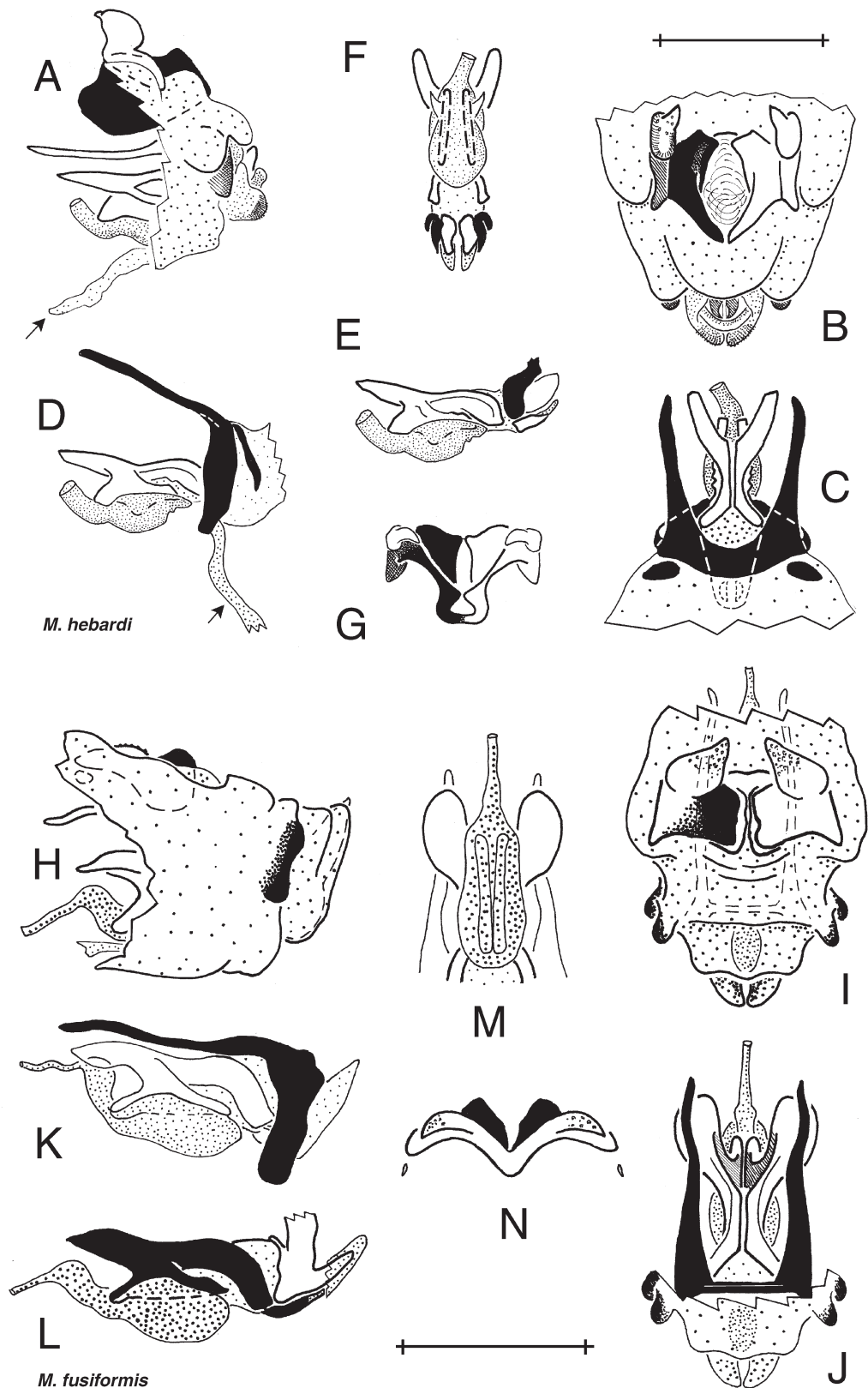
K: endophallus, cingulum (black) and aedeagal valves.

L: endophallus (black), arch and superior aedeagal valves.

M: endophallus (in part), ventral view.

N: epiphallus, axial view.

* This is a tongue of unsclerotized membrane attached to or near the ventral extremities of the rami, probably derived from the ectophallic membrane, and in the undissected phallus it runs anteriorly, directly under the ejaculatory sac. It has been frequently figured previously in other acridoids, especially by Descamps (see e.g., his Figs 19 & 27 (1977a), Fig. 80 (1977b) or Figs 80 & 118 (1978), but as far as I know never named or mentioned in text. My assertion that it is a "retractor apodeme" is speculation based on its form and position, I have performed no experiments to determine its function in the intact animal.



anterior parts of lateral margins variably melanized. Male cercus short and deep in lateral view, at the tip sometimes bifurcate: the outer process always very short, usually completely obsolete, the inner long, with a melanized chisel-shaped tip, inflected upwards and inwards by up to 90° giving a hook-like structure. [Amédégnato (1977) interprets this as being the modified internal apophysis of the cercus, the rest of which has disappeared]. Basally and dorsally, two other short melanised processes. Subgenital plate laterally compressed, pointed or rounded in lateral view.

Female supra-anal plate (Fig. 9) elongate, lozenge-shaped with a rounded tip, tectate proximally. Cerci extremely short and blunt. Ovipositor valves short and strongly hooked, laterally compressed; dorsal valve with interior dorsal edge much higher than exterior, ventral valve with a long concave space between the first and subsequent teeth (diastoma); retractable. Subgenital plate simple, with subrectangular shoulders flanking a thin, transparent, upwardly inflected and acutely pointed egg-guide which protrudes behind the lower ovipositor valves when these are retracted, curling upwards behind their tips. The entire female genital complex is densely haired (for clarity's sake not shown in the Figures presented here).

Internal genitalia.—

Male (Fig. 8). Lophi of epiphallus reduced to concave, melanised, plate-like thickenings of the bridge. Ancorae weakly sclerified, large,

pointed. Oval sclerites very small, in some specimens absent. Ectophallic membrane posterior to epiphallus thickened and sometimes weakly sclerotized. Lateroventral sclerites small, forming vertical flaps of membrane on either side of the aedeagus, the inner surfaces weakly sclerotized. Cingular apodemes and zygoma reduced to thin rodlike structures, somewhat wavy, arranged orthogonally; rami well developed, encircling the aedeagus almost completely, with a large sheet-like membranous apodeme inserted ventrally and running anteriorly. Arch sclerite well developed, dorsal aedeagal sclerites short, upwardly slanted. Partially sclerified ectophallic membrane integrated into both ventral and dorsal aedeagal valves and is their main component.

Endophallic apodemes flattened dorsoventrally and widely separated at their tips. Middle part of endophallus also dorsoventrally flattened, extending laterally over the walls of the spermatophore sac. Gonopore processes elongated longitudinally, extending over almost the whole length of the ejaculatory sac (Figs 8L, 8M). Flexure very short, completely fractured. Ventral aedeagal sclerite rudimentary, with a short membranous continuation, usually shorter than the dorsal valve.

Female (Fig. 9). Post-vaginal sclerites lacking columellae. Bursa copulatrix simple, a short thin-walled ampulla; duct long and thin, widening distally towards the spermatheca; lateral diverticulum of spermatheca very short, apical diverticulum long and sausage-shaped, bent back on its self towards its tip.

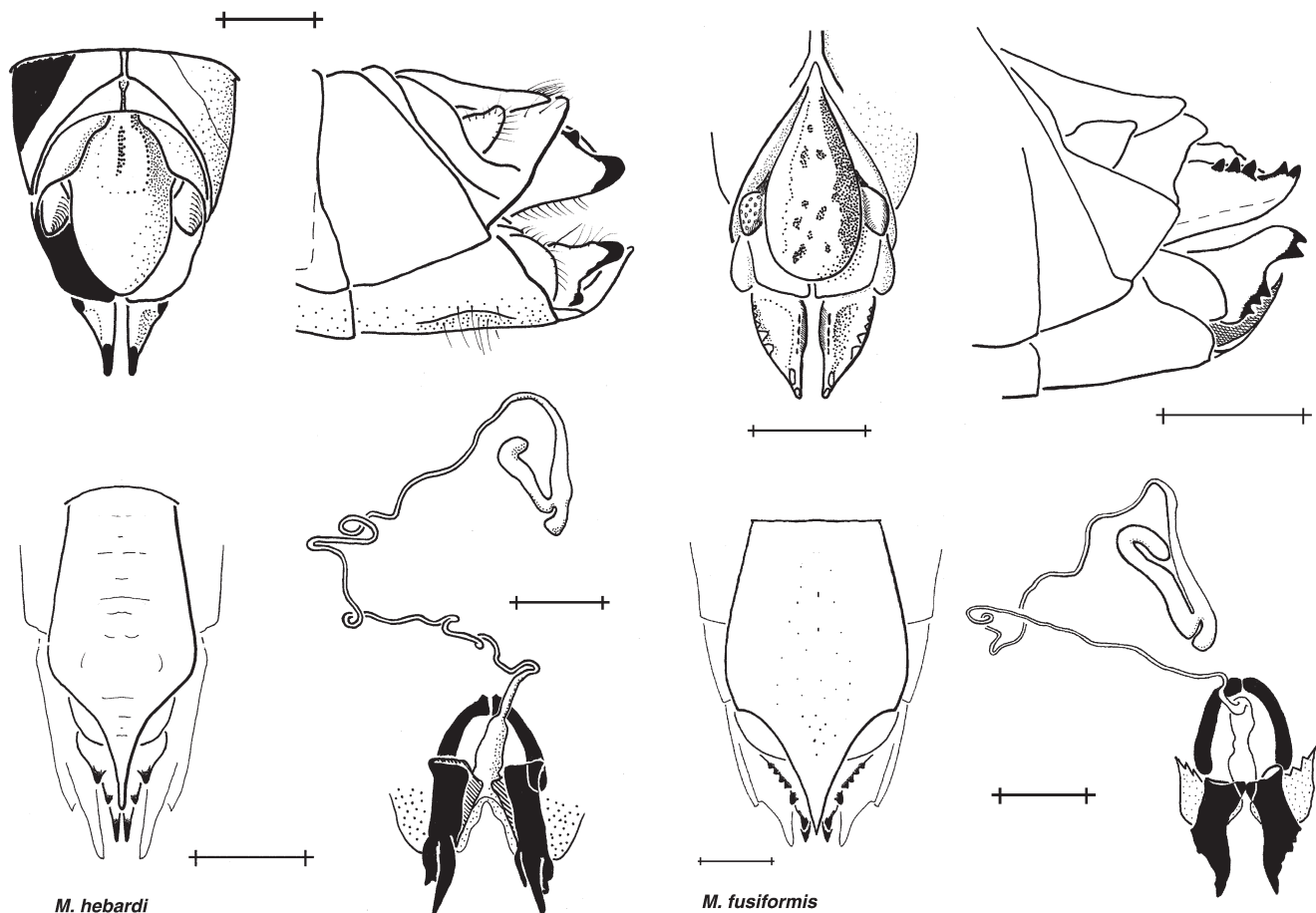


Fig. 9. Female genitalia of *M. hebardii* (left hand side) and *M. fusiformis* (right hand side). Scale bars: 1 mm. Clockwise for each species: dorsal view, lateral view, spermatheca and bursa copulatrix; subgenital plate. In both species the ovipositor valves are almost completely retractable into the abdomen, when contracted, the egg guide forms the most posterior extremity.

Range.— S. Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, W. and Central Panama, between 8° and 18° N. Not as yet recorded from Belize or El Salvador, nor from Colombia or elsewhere in S. America.

1. *Microtylopteryx hebardii* Rehn 1905
(Fig. 6A)

Rehn 1905: 448.

Type locality.— Carrillo, Prov. S. José, Costa Rica.

Location of type specimen: ANS Philadelphia.

Hebard 1924: 137 (designation of type specimen).

Rehn 1929: 58.

Rehn 1955: 1213.

Braker 1989.

Braker 1991.

Braker and Chazdon 1993.

Synonymy.—

= *M. h. caligo* Rehn 1955: 123. **new syn.**

= *M. nigrigena* Hebard 1924: 137, new status (see below).

Etymology.— Named for Morgan Hebard, Philadelphian orthopterist of the first half of the 20th century.

Diagnosis.— Antennal flagellum with 18 to 21 segments, proportionately nearly twice as long in males as in females. Fastigium (Figs 1 and 2) short, 0.45× as long as wide at the base, sloping steeply downwards, concave, grooved distally in the midline. Posterior margin of prothorax (Fig. 1, P) broadly incised medially, anterior margin usually entire. Posterior angle of prothoracic lobe contrastingly colored gold. Tegmina (Fig. 1, Teg) narrow and strap-like, not more than 15% as wide as long, covering only the upper edge of the tympanum, and of variable length, usually extending to the posterior margin of the 1st abdominal tergite. Leading edge darker colored than trailing edge. Abdominal segments 3 and 4 with prominent paired gold spots laterally. Hind femur relatively long [F/P = 2.93 to 3.4 (females), 3.24 to 3.62 (males)] and slender (F/FD = 4.4 to 5.1×). Internal face of hind femur dark brown distally, blackish proximally, with no pale bands. Hind foot formula 35:10:55.

Male subgenital plate (Fig. 7) pointed with a straight dorsal border. Female subgenital plate (Fig. 9) boat-shaped, nearly twice as long as the preceding sternite, posterior margin tapering smoothly to a pointed egg-guide. Ovipositor valves with blunt, squared-off teeth — this is related to the oviposition habit (see Natural History below). Anterior apodemes of endophallus not especially widened at their tips (Fig. 8C); ectophallic membrane posterior to epiphallus forming a “nose” overhanging the aedeagus in the retracted state (Figs 8A, B). Bridge of epiphallus deeply depressed, forming a bowl-like structure (Figs 8A, B, G).

Dimensions.— see Table 1. Sexual dimorphism ($P_{\text{male}}/P_{\text{female}}$) = 0.71 in both subspp. After normalization to P, males have relatively slightly shorter abdomina, much longer antennae (1.9×), a narrower interocular space (0.9×), slightly longer hind legs (1.1×) and more protuberant eyes (1.1×). In both sexes the length of the antennal flagellum is the most variable character.

Larval coloration.— Young larvae have a quite different coloration from the adults. Antennae, head, mouthparts, prothorax, all entirely

black except a) eyes are dark brown and b) post ventral angle of pronotum is pinkish yellow. Fore and mid legs, dull pale green with brown banding; coxae yellow mottled pink-brown. Terga of T2-3 and A1-3, leaf green dorsally, more distal segments with olive brown mottle. Abdominal terga black laterally, A4 & 5 bearing showy paired yellow spots by instar III. Thoracic epimera and episterna pale brown with yellow marks. Cerci thick at base, abruptly constricted to long fine yellowish points. Hind femur, lateral and ventral external faces black, dorsal external face olive brown. Tarsi and feet blackish brown, tibial spines black. Knee brown above, ventral lobe black.

Distribution.— (Fig. 10A) Costa Rica, on the Caribbean slope only, from N of the Río Reventazón and including the Cordillera del Norte, to at least Central Nicaragua. Apparently absent from SE Costa Rica and W Panama.

Natural History.— Possibly the best known Neotropical grasshopper in respect to food plant selection and oviposition, largely due to the work of H.E. Braker. Ecologically very different from the sympatric *M. fusiformis*. *M. hebardii* is an oligophage on broad-leaved monocots (Araceae, Marantaceae, Heliconiaceae). The eggs are laid endophytically in the rhachis of the leaf; the female first bites a hole in outer wall of the rhachis, then inserts the abdomen into this hole. This presumably explains the relative regression of the ovipositor teeth. The larvae are subsocial and remain grouped throughout their larval history, often on a single leaf, which can be severely damaged at the end of their development. In undisturbed forest associated especially with understorey palms such as *Geonoma cuniata*, *G. congesta*, *Asterogyne martiana*, *Chamaedorea exorrhiza* and *Synecanthus warscewicziana*. In disturbed or wetter areas *Heliconia* or *Calathea* or *Maranta* spp. are used. Adults are occasionally seen feeding (but not ovipositing) on a variety of other plants, such as *Vriessia* (Bromeliaceae) or domestic banana (Musaceae).

1A. *Microtylopteryx hebardii nigrigena* (Hebard 1924), new status
(Fig. 6B)

Microtylopteryx nigrigena Hebard 1924: 137.

Type locality.— Panama: Prov. Colón: Gatún.

Location of type specimen: ANS Philadelphia.

Etymology.— Latin *nigrum*, black; *gena*, cheek.

Diagnosis.— Differs from the nominate race of the species as follows: about 12 to 15% smaller, hind femora of males relatively shorter (see Table 1). (In the few specimens available, frontal ridge more deeply grooved between the antennae than in *M. hebardii*, and male furcula with more acute outer angles than in *hebardi*, but these may be individual characters). Other differences are in coloration. In males, the face and genae are solid dark brown (as in the females of both subspecies), and not yellow or cream as in *h. hebardii*; meso- and metathoracic pleura mostly black rather than brown. Antennal flagellum of both sexes with 18 segments, predominantly white, with a short black band proximal to the white 13/14th segments, and black segments distal to them. The gold marks of *M. hebardii* are replaced by white or cream in *nigrigena*, and the undersides of the tarsal pads and the arolia are also white. The leading (ventral) edge of the tegmen is pale, not dark. Inner face of hind femur pale proximally, darkening distally, and the proximal part of the ventral outer surface is blueish rather than dark green.

Dimensions.— see Table 1.

Distribution.— (Fig. 10A) Known only from the type series, plus two females (CAS) from same locality, and a single pair from Cerro Copé, Prov. Choclé (GBFM). As these are some of the best collected areas in Panamá, the species must be very infrequent.

Natural History.—Unknown. The close morphological similarity to *hebardii* suggests that the two subspecies are ecologically similar, but there is no evidence.

2. *Microtylopteryx fusiformis* Rehn 1905 (Fig. 6C)

Rehn 1905: 451.

Type locality.— Carrillo, Prov. S. José, Costa Rica.

Location of type specimen.— ANS Philadelphia.

Synonymy.—

=*M. talamancae* Rehn 1929: 53, new syn.

=*M. tristani* Rehn 1929: 55, new syn.

=*M. f. lamprus* Rehn 1929: 51, new syn.

Etymology.— Latin *fusus*, spindle; *fusiformis*, spindle-shaped.

Based on the foregoing analysis, I redefine this taxon to include all known *Microtylopteryx* (*Tristanacris*) sensu Rehn. Three local subspecies (*M. f. worthi* new status, *M. f. chiapensis* new status and *M. fusiformis fastigiata* new ssp.) can be distinguished morphologically from the mass of the rest (*M. f. fusiformis*, new status) (below).

Diagnosis.— Medium-small, L = 13.2 to 14.6 mm, F = 7.32 to 10.5 mm (males); L = 15.65 to 23.85 mm, F = 9.56 to 11.21 mm (females). Antennae short-medium, 16 flagellar segments, the widest being nos 12 to 15. Fastigium (Figs 3 and 4) horizontal, triangular, flat or convex dorsally, at the tip often but not always incised by the groove of the frontal ridge. Vertex with or without a medial raised carina. Anterior margin of pronotum usually emarginate or notched in midline; posterior margin not deeply incised in midline. Posterior angle of prothoracic lobe not of a contrasting color. Tegmina (Fig. 5) spatulate, about 35% as wide as long at their broadest point, usually covering the tympanum and often extending briefly into A2. Hind femur relatively short, F/P = 2.22 to 3.20. Foot formula usually 38:14:48, except in ssp. *fastigiata* (see below)

Male supra-anal plate (Fig. 7) with proximal margins somewhat turned upwards and melanized, distal margins simple, densely haired (hairs not shown in Fig. 7). Male subgenital plate laterally compressed, rounded in lateral view, with a sulcus bounded by two ridges medially on the dorsal edge. Anterior apodemes of endophallus with the tips noticeably widened (Figs 8J, M); ectophallic membrane posterior to epiphallus forming a straight fold, but not a pointed nose (Fig. 8I).

Female subgenital plate (Fig. 9) not much longer than the preceding sternite, smoothly polished, posterior margin bisinuate, with a rectangular lobe either side of the triangular medial egg guide. Ovipositor valves sharply toothed, the upper valve with a chisel-shaped tip. The valves can be facultatively retracted into the abdomen, in which case the egg-guide projects beyond them and

forms the most posterior part of the abdomen.

Coloration varies from nearly completely black in some montane localities to pale brown with conspicuous black, dark brown and gold markings. Internal face of hind femur usually light brown with transverse black bands, but can be completely black or completely brown. There is great variation between populations in size (high altitude specimens are smaller, and the largest individuals are 1.4× larger than the smallest), in the length of the fastigium and tegmen, and the development of the median crests of head, pronotum and abdominal segments (see Figs 3-5).

Dimensions.— see Table 1. Sexual dimorphism ($P_{\text{male}}/P_{\text{female}}$) = 0.75, varying from 0.73 to 0.78 in different populations, and thus slightly less than in *M. hebardii*. After normalizing, males have slightly shorter abdomina, longer antennae (1.3 to 1.6×), a narrower interocular space (0.8 to 0.9×), slightly longer hind legs (1.02 to 1.17×) and more protuberant eyes (1.08 to 1.14×).

Larval coloration.—Very young larvae (I and II) are dark brown with black abdomen and hind legs; all of face (except eyes) and antennae creamy white; hind femur with white bands and/or spots. Later larvae (III or IV) blackish; abdominal tergites begin to show adult pattern; face and hind leg marking duller than before; antennae longer, brown with white band as in adult. All stages have a white postgenicular ring around the upper hind tibia.

Range.— (Figs 10B, C) Wet forest from Central Panama (Veraguas Province) to Southern Mexico (Chiapas). Absent from the Pacific lowlands of Panama and from the dry forest zone of Western Costa Rica.

Natural history.— Typical of leaf litter and low understorey plants within and at the edges of wet forest. Probably a generalist; plants fed on in the wild include *Liabum bourgeauii* (Asteraceae), *Alloplectus* sp. (Gesneriaceae), *Pila* sp. and *Urera baccifera* (Urticaceae), *Ruellia* sp. and *Blechum brownei* (Acanthaceae), and a commelinaceous plant. Larvae are solitary. Details of oviposition behavior unknown, but the much more robust ovipositor (see Fig. 9) suggests a different method than that of *M. hebardii*.

2A. *M. fusiformis chiapensis* (Rehn), new status

M. chiapensis Rehn 1955: 114.

Type locality.— Mexico: Chiapas, Sierra Madre del Sur, Vergel; 800 m.

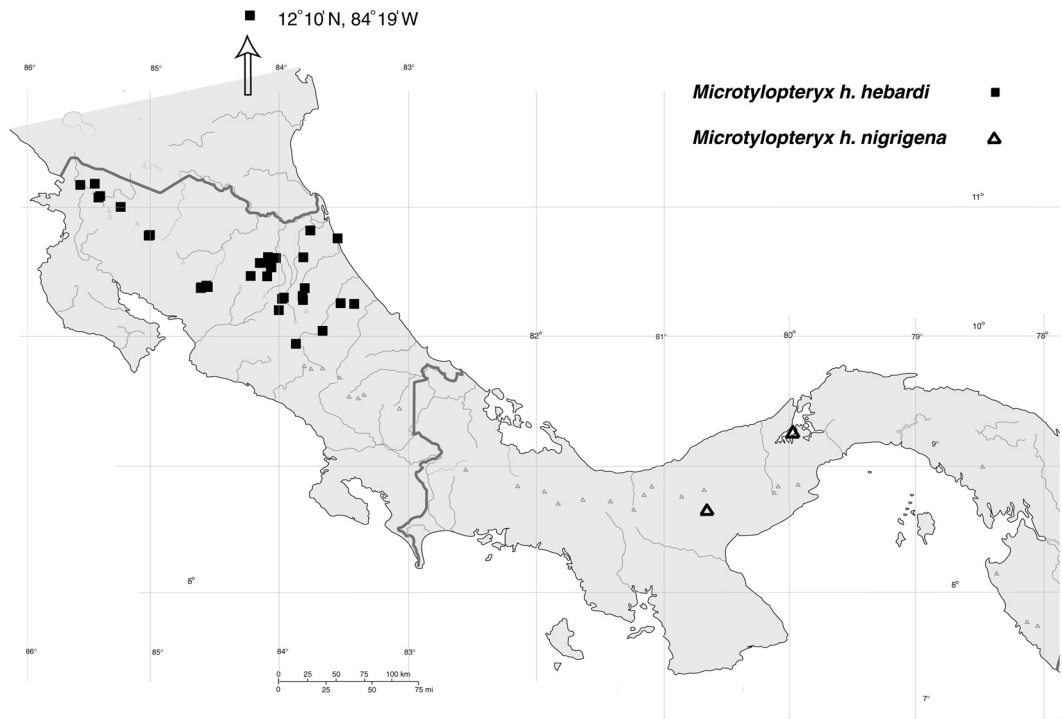
Location of type specimen.— ANS Philadelphia.

Diagnosis.— Proportionately longer femora; $F_{\text{male}} = 2.81$ to $3.20\times$ as long as pronotum, $F_{\text{female}} = 2.46$ to $2.98\times$; sexual dimorphism in femur length is more pronounced ($1.17\times$ on average) than in other populations. Fastigium short and broad, Fast L/P 0.14 to 0.17 (barely overlapping the range of *worthi*, 0.10 to 0.15, but usually more narrowly notched at the extremity of the fastigium (Figs 4A, 5) than in *worthi*). Small in size, $P_{\text{male}} = 2.61$ to 3.08 mm, $P_{\text{female}} = 3.32$ to 3.86 mm.

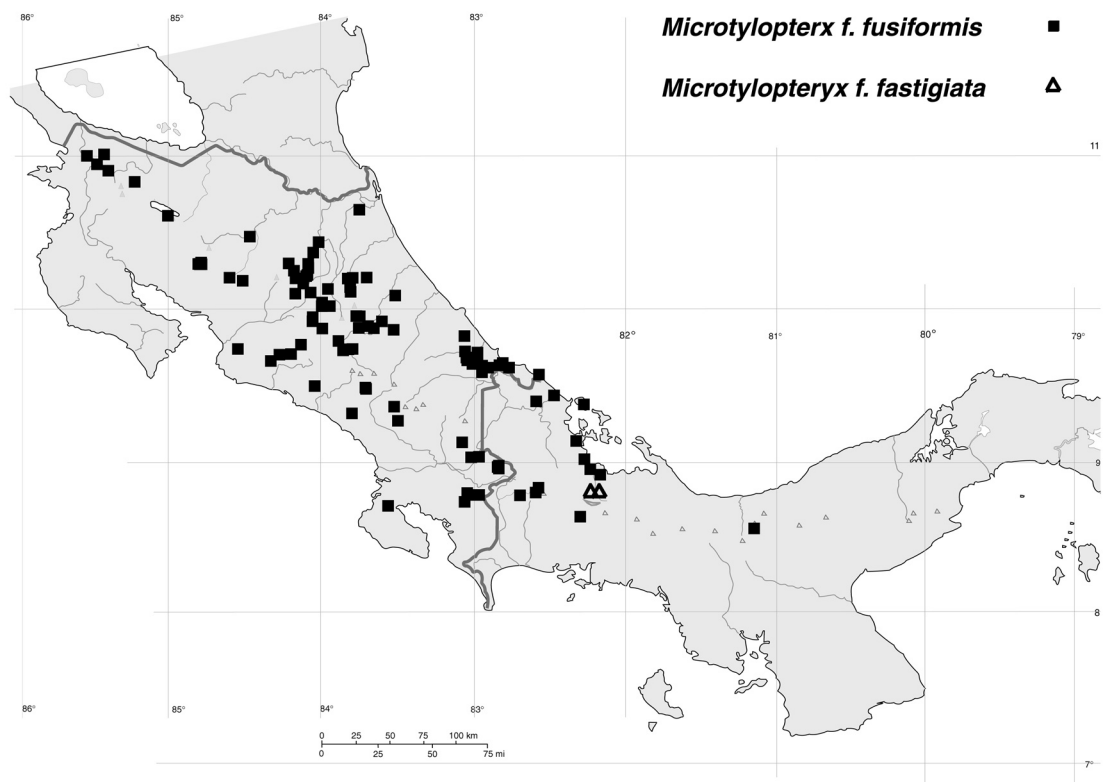
Distribution.— (Fig. 10C) Guatemala, S. Mexico (Chiapas)

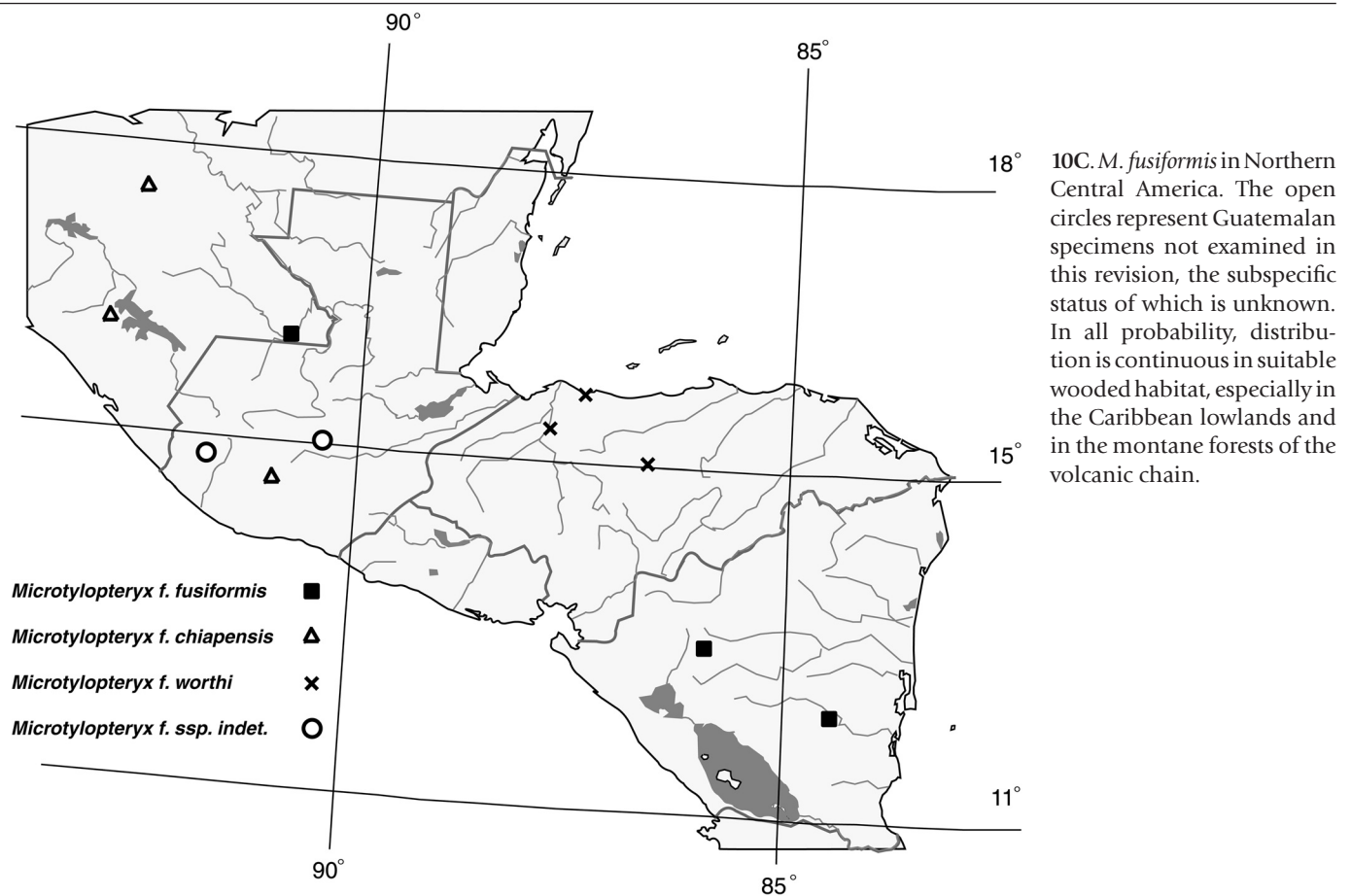
Fig. 10. Distribution maps.

A. Known localities of *Microtylopteryx hebardii* and *M. hebardii nigrigena*. Note the disjunct distribution of the 2 subspecies.



B. *M. fusiformis* in Costa Rican and Panama. Note absence from the dry woodland areas of the Pacific lowlands. The Caribbean watershed, between the most easterly population (Veraguas, Panama) and the other populations has not been sampled; East of Veraguas the genus has been sought, but not found.





2B. *M. fusiformis worthi* (Rehn), new status

M. worthi Rehn 1955: 117.

Type locality.— Honduras: Atlantida District, near Tela, Lancetilla.

Location of type specimen.— ANS Philadelphia.

Diagnosis.— Fastigium (Figs 3, 5) very short and broad (Fast L/B 0.36 to 0.47 in both sexes), usually broadly grooved at the apex. Micropterous in some populations, including at the type locality, elytron then not extending beyond the posterior margin of the metathoracic tergum; brachypterous in other populations (Fig. 5). Antennae relatively very long (1.82 to 2.30P in males, 1.31 to 1.45P in females). Fairly large for the species, $P_{\text{male}} = 2.98$ to 3.93 mm, $P_{\text{female}} = 3.63$ to 4.26 mm.

Distribution.— (Fig. 10C) Caribbean slope of Northern Honduras, from sea level to at least 1500 m.

**2C. *M. fusiformis fastigiata* new ssp.
(Fig. 6C)**

Holotype.— Panama, Prov. Bocas del Toro: 1.3 km past watershed on road Fortuna-Chiriquí Grande, 850–1035 m, 23.9.1997 (Rowell CHF & Bentos-Pereira A), specimen no. 97465 (ANS Philadelphia).

Paratypes.— **Males**: as holotype, specimen nos. 97489, 97439 (both

ANSP), 97479 (MNHN); 18. Sept. 1999, specimen nos. 99123 (RC), 99133 (MNHN); Quebrada Felix, 2 km NW of summit of road to Chiriquí Grande, 900 m, 26. September 1997 (Rowell CHF & Bentos-Pereira A), specimen no. 97540 (RC); 19. September 1999, specimen no. 99173 (GBFM). **Females**: as holotype, but 26. September 1997, specimen nos 97537, 97555 (both ANSP), 97552 (RC); Quebrada Felix, 2 km NW of summit of road to Chiriquí Grande, 900 m, 19. September 1997 (Rowell CHF & Bentos-Pereira A), specimen nos 99158 (MNHN), 99171 (GBFM).

Etymology.— Latin *fastigium*, gable; *fastigiata*, having a gable; in this context referring to the long fastigium of the head.

Diagnosis.— Differs from other populations of *fusiformis* in having a very long fastigium (Fast L/B = 0.88 to 1.06) and an unusually serrated profile of the pronotum and first abdominal terga in lateral aspect (Figs 3, 4, 6A). First and second tarsal segments of hind foot shorter than in other races, so that Ta3 comprises 53 to 54% of the foot. Includes the largest individuals so far recorded for the species; $P_{\text{male}} = 3.7$ to 4.13 mm, $P_{\text{female}} = 4.74$ to 5.23 mm.

Distribution.— (Fig. 10B) Montane forest of Caribbean slope of Prov. Bocas del Toro, from 1100 to about 500 m. altitude.

Key to species and subspecies (see also Figs 6, 7, 9).

1. Body shape cylindrical, not narrowed anterior to insertion of hind femora. Antennal flagellum with 18 or more segments. Anterior

margin of pronotum not emarginate in midline; posterior angle of pronotum light in color. Tegmina narrow, with parallel margins. Hind femur at least $3.20\times$ (males) or $2.93\times$ (females) length of pronotum *Microtylopteryx hebardii* (2)
 — Body shape fusiform, widest in dorsal view at insertion of hind femora, narrowed anterior to this point. Antennal flagellum with 16 or fewer segments. Anterior margin of pronotum usually at least minutely emarginate in midline; posterior angle of pronotum not light in color. Tegmina spatulate, margins diverging distally. Hind femur never more than $3.20\times$ (males) or $2.98\times$ (females) length of pronotum, usually less. *Microtylopteryx fusiformis* (3)

2. Subspecies of *hebardi*:

— Lower proximal surface of hind femur tinged with dark green. In male, entire lower face pale yellow. F/P always exceeding 3.30 (males) or 3.00 (females). N.E. Costa Rica, E. Nicaragua. . . . *M.h. hebardii*.
 — Lower proximal surface of hind femur tinged with blue. In male, entire lower face dark brown. F/P never exceeding 3.30 (males) or 3.00 (females). Central Panama. *M. h. nigrigena*.

3. Subspecies of *fusiformis*:

— Usually small in size, $P_{\text{male}} = 2.61$ to 3.08 mm, $P_{\text{female}} = 3.32$ to 3.86 mm. Proportionately long femora; $F_{\text{male}} = 2.81$ to $3.20\times$ as long as pronotum, $F_{\text{female}} = 2.46$ to $2.98\times$; sexual dimorphism in femur length is more pronounced ($1.17\times$ on average) than in other populations. Fastigium rather short and broad (Figs 3, 4), Fast L/B 0.40 to 0.50 in both sexes, overlapping the range of *worthi*, but usually more narrowly notched at the extremity of the fastigium. Guatemala, S. Mexico *M.f. chiapensis*.
 — $P_{\text{male}} = 2.98$ to 3.93 mm, $P_{\text{female}} = 3.63$ to 4.26 mm. $F_{\text{male}} 2.54$ to $2.97\times$ length of pronotum, $F_{\text{female}} 2.42$ to $2.55\times$. Fastigium very short and broad, usually broadly grooved at apex (Fig. 5), Fast L/B $= 0.36$ to 0.47 in both sexes. Antennae rather long, 1.82 to $2.30P$ in males, 1.31 to $1.45P$ in females. In some populations (Tela), but not all, tegmina very short, not exceeding posterior margin of metathorax, leaving tympanum uncovered (Fig. 5). Northern Honduras. *M.f. worthi*.
 — Large in size, $P_{\text{male}} = 3.7$ to 3.92 mm, $P_{\text{female}} = 4.74$ to 5.23 mm. $F_{\text{male}} 2.41$ to $2.66\times$ as long as pronotum, $F_{\text{female}} = 4.74$ to $5.23\times$. Fastigium very long and narrow (Figs. 3, 4), Fast L/B $= 0.88$ to 1.06 in both sexes. Last tarsal segment of hind foot longer than in other subspecies (53 to 54% of foot). Western Panama, highlands of Bocas del Toro *M.f. fastigiata*.
 — $P_{\text{male}} = 2.61$ to 4.13 mm, $P_{\text{female}} = 3.87$ to 5.39 mm. F_{male} maximally $2.8\times$ length of pronotum, F_{female} maximally $2.67\times$. Fastigium of variable size and shape (Figs 3, 4), fastigium L/B $= 0.44$ to 0.86 in both sexes. Does not show the characters of the preceding 3 subspecies. Central Panama, through Costa Rica, to at least Central Nicaragua, probably extending to Mexico *M.f. fusiformis*.

Discussion

The picture that emerges from this analysis is of 2 widely distributed flightless species, each consisting of a geographical mosaic of local populations which are slightly but measurably differentiated from each other, but overlapping in the range of almost all characters. This picture applies especially to the more widely and continuously distributed *M. fusiformis*. Within each of the two species there is no genitalic differentiation.

Such a situation poses problems for the taxonomist. In an ideal world, species status in taxonomy would represent biological species, i.e., those with pre- or postzygotic reproductive isolation, just as systematics would represent phylogeny. In the real world, however, we do not normally have the necessary knowledge, and proxies must be used instead. In grasshopper taxonomy, repeatable differences in the morphology of the reproductive system are used as a proxy for prezygotic isolation, and normally warrant species status. Unfortunately the reverse is not necessarily true; not all reproductively isolated populations can be assumed to have developed different genitalia, and in some groups there is remarkably little genital differentiation. Within the Ommatolampinae, however, male genital differentiation is normally well developed, and the absence of differences between the genitalia of the various populations of the 2 species of *Microtylopteryx* is taken to indicate that they are all conspecific. This is supported by the fact that different local forms are allopatric, and there are no obvious differences between them in ecology. That is, there is no *a priori* ecological or behavioral evidence for reproductive isolation.

The fact that the local populations are all significantly different from each other statistically in some way, probably implies some degree of genetic differentiation. When is it useful to recognize subspecific divisions? I have here taken the position that a subspecies is a local population showing morphological differences large enough that all its members can be unambiguously assigned to it and differentiated from all other subspecies. This at least makes the category taxonomically practical and potentially useful. Those populations for which this is not possible are lumped together as the nominate race. Clearly this is a system of convenience, which says nothing about the degree of genitalic difference between the populations. *M. hebardii nigrigena* and *M. fusiformis fastigiata* are readily identifiable forms and pose no problems as subspecies. *M.f. chiapensis* and *M.f. worthi*, on the other hand, are borderline cases, and distinguishing characters are difficult to find. I leave them as distinct taxonomic entities for the present, largely because we know so little about the faunas in which they occur. If we had the same sampling density in Honduras and Guatemala and Chiapas that we have in Costa Rica and Panama, it might well be that they would merge with *M. fusiformis fusiformis*.

Several of Rehn's original species and subspecies of *Microtylopteryx* are here synonymized because a) the differences he described are either not substantiated or are trivial relative to the degree of variation which occurs, b) many of his sample sizes were quite inadequate to distinguish between intra- and extrapopulation variability, and c) there is no genitalic differentiation. Some of the distinctions proposed by Rehn are real, some are not — the problem was the small sample sizes involved in most cases, and the failure to use a statistical approach when dealing with a variable population. It should be recalled that statistical techniques were in their infancy when Rehn commenced his career, and he never adopted them in later life.

Finally, Rehn's and Hebard's original samples were collected between 100 and 80 years ago. The additional material from the same localities analysed here dates from the last 3 decades of the 20th century. The time interval has thus been 50 to 100 years, corresponding to at least that many generations of grasshoppers. It is therefore of some interest that, where the data are adequate to allow comparisons, there has been no change in the detailed morphometrics of the populations during that time: the local morphologies are apparently stable.

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Appendix 1. Synopsis of Rehn's (1905, 1929, 1955) diagnoses (using his taxonomy). He tended to contrast pairs of taxa, as shown in the paragraph grouping below.

Microtylopteryx (*Microtylopteryx*)

Body shape elongate, not widened at insertion of femora. Fastigium in outline not sharply trigonal, broadly emarginate mesad in dorsal view. Dorsal surface not convex, groove broad. Fastigio-facial angle narrowly rounded rectangulate. Pronotum hardly at all tectate. Anterior margin of pronotum not emarginate mesad. Median carina arcuate in the metazona, disk less strongly broadening caudad. Tegmina narrow, lanceolate. Hind femora hardly inflated, elongate.

Microtylopteryx (*Tristanacris*)

Body shape fusiform, widened at insertion of hind femora in dorsal view. Fastigium in outline sharply trigonal in dorsal view. Dorsal surface convex; terminal groove narrow, subfissate. Fastigio-facial angle rounded acute. Pronotum strongly tectate. Anterior margin of pronotum narrowly emarginate mesad. Median section more regularly elevated caudad, disc strongly broadening caudad. Tegmina spatulate. Hind femora inflated when seen in dorsal or lateral view, short.

Subdivisions of *Microtylopteryx* (*Microtylopteryx*)

M. hebaridi. Head broader in both sexes. Limbs longer, especially hind one. Male with face and genae light yellow. Tegmen bicoloured.

M. nigrigena. Head narrower in both sexes. Limbs shorter. Male with face and genae fuscous. Fastigium slightly shorter than in *hebaridi*. Tegmen unicoloured. Cerci shorter, more suddenly reflexed.

M. hebaridi hebaridi. Eyes more protuberant: head narrower across the genae. Hind metatarsus shorter. Dorsal profile of fastigium less downward sloping. Fastigiofacial angle less broadly rounded.

M. hebaridi caligo. Eyes less protuberant: head broader across the genae. Hind metatarsus longer. Dorsal profile more downward sloping. Fastigiofacial angle more broadly rounded.

Subdivisions of *Microtylopteryx* (*Tristanacris*)

M. fusiformis and *M. talamancae*. Head and anterior pronotum less compressed. Colour brighter, more patterned. Male cerci less recurved dorsally. Fastigium less produced in both sexes, moderately acute in female. Hind femora very inflated and more bullate, greater in depth.

M. tristani. Head and anterior pronotum more compressed. Colour duller, more uniform. Male cerci more recurved dorsally. Fastigium more produced in both sexes, decidedly acute in female. Hind femora less inflated, narrower. Medial carina more arcuate.

M. fusiformis. Head broader in both sexes. Male cerci less recurved dorsally. Fastigium wider at base than long.

M. talamancae. Head narrower in both sexes. Male cerci more recurved dorsally. Fastigium width and length subequal (i.e. narrower and/or longer than in *fusiformis*). Medial carina less arcuate.

M.f. fusiformis. Eyes more protuberant, laterally and dorsally. Ventral section of face more deplanate. Profile concave ventrad of fastigium. Fastigium with lateral margins concave in dorsal view.

M.f. lamprus. Eyes less protuberant, laterally and dorsally. Ventral section of face less deplanate. Profile straight ventrad of fastigium. One presumes further: fastigial margins not concave.

M. chiapensis (relative to *worthi* and *fusiformis*). Male cerci more recurved dorsally. Breadth across genae less than *fusiformis*. Antennae shorter and stouter. Fastigium broader than long, more obtuse than 90°, lateral margins not concave in dorsal view. Tegmina normal. Femora more slender less inflated.

M. worthi (relative to *chiapensis*). Male cerci less recurved dorsally, more "distad" (?). Head as in *fusiformis*. Interocular space larger. Antennae longer than *chiapensis* or *fusiformis*. Lateral facial carinae more evident than *fusiformis*. Very short and broad fastigium. Tegmina short, do not extend beyond metanotum. Hind femora less attenuate than in *chiapensis*.

Appendix 2. Example of the comparison of 2 large samples. Sample 1 consists of all males from Costa Rican and Panamanian populations apart from Highland Bocas del Toro, and represents *M. fusiformis fusiformis* Rehn in the sense of this article. Sample 2 consists of all males from Northern Honduras. It includes both the Tela population, which has very short tegmina, and those from other localities, which have normal ones; for this reason the means, standard deviations and “t” values are not calculated for this character (gaps marked with the symbol §).

The comparison (3.) shows that there are significant differences between the two samples in the averages of about half of all characters (P= 0.05 or less). However, their ranges overlap in all cases (compare “Maximum” and “Minimum” values for the two samples). Only the normalized fastigium length (Fast L/P) and the ratio of fastigium length to breadth (Fast L/B) show extremely little overlap, which itself may well be due to experimental error. This lack of overlap justifies subspecific rank for sample 2 (*M. fusiformis worthi*), as these two characters distinguish all individuals drawn from either sample.

Microtylopteryx (Tristanacris) Males

	Character	1. Combined Costa Rica and Panama sample						2. Combined Northern Honduras sample						3. Comparison of 1. with 2.			
		Mini- mum	Maxi- mum	Mean	SD	SD/ mean	N	Mini- mum	Maxi- mum	Average	S.D.	S.D./ average	N	Student's "t"	d of freedom	Significant?	over- lap?
Raw data: values in millimetres	P	2.81	3.92	3.42	0.27	0.08	100	2.98	3.93	3.55	0.26	0.07	14	1.66	112	nsd	y
	L	10.70	15.80	13.54	1.03	0.08	100	12.95	15.27	14.13	0.76	0.05	14	2.03	112	?*	y
	Ant	3.68	7.96	5.41	0.87	0.16	93	6.18	7.86	7.06	0.53	0.07	9	5.54	100	**	y
	IOS	0.35	0.70	0.56	0.07	0.13	100	0.48	0.73	0.56	0.07	0.12	14	-0.14	112	nsd	y
	E-E	2.60	3.59	3.08	0.21	0.07	100	3.03	3.60	3.30	0.15	0.05	14	3.75	112	**	y
	Fast B	0.79	1.23	1.05	0.10	0.01	100	0.95	1.15	1.04	0.05	0.05	14	-0.35	112	nsd	y
	Fast L	0.45	0.86	0.65	0.08	0.13	100	0.37	0.50	0.42	0.04	0.08	14	-10.10	112	**	y
	C-V	2.66	3.68	3.23	0.19	0.06	100	3.12	3.92	3.42	0.21	0.06	14	3.36	112	*	y
	G-G	2.16	3.08	2.65	0.21	0.08	100	2.64	3.05	2.78	0.12	0.04	14	2.28	112	?*	y
	F	7.32	10.50	8.81	0.63	0.07	100	8.84	10.64	9.75	0.52	0.05	14	5.30	112	**	y
	FD	2.01	3.15	2.57	0.24	0.09	100	2.41	2.86	2.62	0.13	0.05	14	0.75	112	nsd	y
	Tegmen	2.09	3.14	2.64	0.24	0.09	100	0.92	2.65				14	§			y
	Ta1	0.85	1.32	1.07	0.09	0.09	100	1.06	1.31	1.17	0.07	0.06	13	3.66	111	**	y
	Ta2	0.27	0.47	0.37	0.04	0.12	100	0.32	0.50	0.42	0.05	0.12	13	4.23	111	**	y
	Ta3	1.09	1.84	1.40	0.13	0.01	99	1.42	1.68	1.52	0.09	0.06	13	2.93	110	*	y
	Ta1+2+3	2.36	3.38	2.84	0.22	0.08	99	2.92	3.27	3.10	0.13	0.04	13	4.17	110	**	y
Normalized data	L/P	3.44	4.42	3.96	0.20	0.05	100	3.52	4.62	3.99	0.30	0.08	14	0.57	112	nsd	y
	Ant	1.18	2.16	1.58	0.20	0.13	93	1.82	2.30	2.04	0.16	0.08	9	6.62	100	**	y
	IOS/P	0.12	0.19	0.16	0.02	0.01	100	0.13	0.19	0.16	0.01	0.09	14	-1.39	112	nsd	y
	E-E/P	0.76	1.00	0.90	0.04	0.05	100	0.86	1.02	0.93	0.05	0.05	14	2.57	112	?*	y
	Fast B/P	0.25	0.36	0.31	0.02	0.08	100	0.27	0.35	0.29	0.02	0.08	14	-1.89	112	nsd	y
	Fast L/P	0.14	0.25	0.19	0.02	0.13	100	0.10	0.15	0.12	0.01	0.12	14	-10.42	112	**	n?
	C-V/P	0.83	1.05	0.95	0.04	0.05	100	0.89	1.12	0.97	0.06	0.07	14	1.44	112	nsd	y
	G-G/P	0.68	0.88	0.77	0.04	0.05	100	0.72	0.90	0.79	0.04	0.06	14	1.00	112	nsd	y
	F/P	2.27	2.80	2.57	0.11	0.04	100	2.54	2.97	2.75	0.15	0.05	14	5.44	112	**	y
	FD/P	0.65	0.85	0.75	0.05	0.06	100	0.65	0.82	0.74	0.04	0.06	14	-0.78	112	nsd	y
	Tegmen/P	0.61	0.94	0.77	0.06	0.08	100	0.28	0.83				14	§			y
	Ta1/P	0.25	0.36	0.31	0.02	0.07	100	0.29	0.40	0.33	0.03	0.09	13	3.10	111	*	y
	Ta2/P	0.08	0.15	0.11	0.01	0.12	100	0.09	0.15	0.12	0.02	0.13	13	3.19	111	*	y
	Ta3/P	0.36	0.53	0.41	0.03	0.07	99	0.38	0.49	0.43	0.04	0.09	13	2.41	110	?*	y
	Ta1-3/P	0.73	0.95	0.83	0.05	0.06	99	0.80	1.00	0.88	0.07	0.07	13	3.64	110	**	y
	Shape ratios	F/FD	3.05	4.17	3.44	0.20	0.06	100	3.47	4.03	3.73	0.19	0.05	14	4.95	112	**
Ta1-3/F		0.29	0.37	0.32	0.02	0.05	99	0.30	0.35	0.32	0.01	0.04	13	-0.24	110	nsd	y
Fast L/B		0.44	0.84	0.62	0.09	0.14	100	0.36	0.46	0.40	0.03	0.09	14	-9.09	112	**	n?
C-V/G-G		1.08	1.44	1.22	0.05	0.04	100	1.17	1.47	1.23	0.07	0.06	14	0.55	112	nsd	y
E-E/G-G		1.00	1.24	1.16	0.04	0.03	100	1.12	1.24	1.19	0.04	0.03	14	2.06	112	?*	y

Raw data		median				median				Symbol	Probability
	Ext spines	5	7	6	102	6	6	6	14	nsd	>0.05
	Int Spines	7	10	9	102	8	9	9	14	?*	≤0.05
										*	≤0.01
										**	≤0.001

Appendix 3. Example of the comparison of a small sample with a larger one. Sample 1 consists of 11 males of *M. hebardii* drawn from at and near the type locality. Sample 2 consists of 4 males from localities in the Cordillera del Norte. As the size of the second sample is so small, means cannot be compared using a t-test. Instead, the 95% confidence limits of the larger sample are calculated ($= \text{mean} \pm 1.96 \times (\text{standard deviation})$) for all characters, and the individual values of the small sample are compared with these limits.

Microtylopteryx hebardii Males

		1. Carrillo and Sarapiquí sample.						2. Cordillera del Norte sample					
Character		Mini- mum	Maxi- mum	Average	S.D.	S.D./ average	N	Lower 95% conf. limit	Upper 95% conf. limit	Sp. No. 97056	Sp. No. 97056	Sp. No. 99468	Sp. No. 99468
Raw data: values in millimetres	P	3.33	3.69	3.54	0.11	0.03	11	3.33	3.76	3.69	3.53	3.60	3.64
	L	14.49	16.94	15.59	0.68	0.04	11	14.22	16.96	16.85	16.88	16.02	15.96
	Ant	6.21	10.89	9.81	1.44	0.15	9	6.93	12.68	10.00	10.88	9.95	9.44
	IOS	0.72	0.87	0.81	0.05	0.06	11	0.71	0.91	0.93	1.00	0.87	0.93
	E-E	3.53	3.78	3.64	0.08	0.02	11	3.48	3.81	3.69	3.68	3.73	3.74
	Fast B	1.13	1.22	1.18	0.03	0.02	11	1.13	1.24	1.28	1.27	1.30	1.27
	Fast L	0.51	0.60	0.56	0.03	0.06	11	0.49	0.62	0.53	0.59	0.56	0.50
	C-V	3.38	3.74	3.53	0.13	0.04	11	3.27	3.80	3.65	3.65	3.50	3.47
	G-G	3.23	3.52	3.36	0.10	0.03	11	3.16	3.56	3.46	3.43	3.45	3.38
	F	11.63	13.08	12.34	0.46	0.04	11	11.42	13.26	12.44	12.39	12.51	12.36
	FD	2.27	2.85	2.64	0.16	0.06	11	2.33	2.96	2.67	2.64	2.81	2.80
	Teg	2.21	2.75	2.55	0.18	0.07	11	2.18	2.92	2.53	2.52	2.83	2.78
	Ta1	1.33	1.49	1.38	0.05	0.03	10	1.28	1.47	1.35	1.41	1.37	1.38
	Ta2	0.33	0.48	0.41	0.05	0.12	10	0.32	0.50	0.43	0.37	0.47	0.40
	Ta3	2.00	2.30	2.15	0.09	0.04	9	1.97	2.33	2.21	2.15	2.20	2.10
	Ta1+2+3	3.76	4.11	3.94	0.13	0.03	9	3.68	4.19	3.99	3.93	4.04	3.88
Normalized data	L/P	4.12	4.59	4.40	0.16	0.04	11	4.09	4.71	4.57	4.78	4.45	4.38
	Ant/P	1.76	3.08	2.76	0.39	0.14	9	1.98	3.55	2.71	3.08	2.76	2.59
	IOS/P	0.21	0.24	0.23	0.01	0.04	11	0.21	0.25	0.25	0.28	0.24	0.26
	E-E/P	0.99	1.07	1.03	0.03	0.03	11	0.98	1.08	1.00	1.04	1.04	1.03
	Fast B/P	0.32	0.34	0.33	0.01	0.03	11	0.32	0.35	0.35	0.36	0.36	0.35
	Fast L/P	0.15	0.17	0.16	0.01	0.05	11	0.14	0.17	0.14	0.17	0.16	0.14
	C-V/P	0.96	1.03	1.00	0.03	0.03	11	0.95	1.05	0.99	1.03	0.97	0.95
	G-G/P	0.90	1.00	0.95	0.03	0.03	11	0.89	1.00	0.94	0.97	0.96	0.93
	F/P	3.34	3.62	3.48	0.01	0.03	11	3.29	3.68	3.37	3.51	3.48	3.40
	FD/P	0.68	0.78	0.75	0.03	0.04	11	0.68	0.81	0.72	0.75	0.78	0.77
	Teg/P	0.66	0.78	0.72	0.05	0.06	11	0.63	0.81	0.69	0.71	0.79	0.76
	Ta1/P	0.37	0.42	0.39	0.01	0.04	10	0.36	0.42	0.37	0.40	0.38	0.38
	Ta2/P	0.09	0.14	0.12	0.01	0.13	10	0.09	0.14	0.12	0.10	0.13	0.11
	Ta3/P	0.57	0.64	0.60	0.02	0.03	9	0.56	0.65	0.60	0.61	0.61	0.58
	Ta1-3/P	1.02	1.14	1.11	0.04	0.03	9	1.04	1.18	1.08	1.11	1.12	1.07
	Shape ratios	F/FD	4.41	5.12	4.68	0.23	0.05	11	4.21	5.14	4.66	4.69	4.45
Ta1-3/F		0.31	0.33	0.32	0.01	0.02	9	0.30	0.33	0.32	0.32	0.32	0.31
Fast L/B		0.43	0.51	0.47	0.03	0.05	11	0.42	0.52	0.41	0.46	0.43	0.39
C-V/G-G		1.03	1.11	1.05	0.02	0.02	11	1.01	1.01	1.06	1.06	1.01	1.03
E-E/G-G		1.05	1.13	1.09	0.02	0.02	11	1.05	1.13	1.07	1.07	1.08	1.11
Raw data				Median									
	Ext spines	6	7	6			11			6	6	6	6
	Int spines	8	9	9			11			8	8	9	9

Appendix 4. Material examined. In view of the large numbers of specimens involved I give here only an abbreviated list, which includes all the known localities, but not all the individual specimens collected at them.

Microtylopteryx hebardii hebardii

COSTA RICA

Alajuela:

Dos Rios, Fca S. Gabriel, LN 318800-383500, May 15, 1990 (Parataxonomos Curso II), specimen no. 0 644822 (INBC); Dos Rios, Fca Aurora, 700-800 m, LN 320000-385000, October 12, 1999 (Rowell CHF), specimen no. 99466 (RC); La Libertad, in valley of R. Caño Negro, between P.N. Rincón de la Vieja and Piedras Blancas, LN 311000-402500, July 21, 1980 (Rowell CHF Rowell-Rahier M), specimen no. 80727 (RC); Laguna Hule, 780-730 m, LN 253900-513700, July 16, 1991 (Rowell CHF), larvae only; R.B. San Ramón, Río S. Lorencito, 1130 m. LN 243900-471000, October 21, 2001 (Rowell CHF) (MUCR); R.B. San Ramón, Río S. Lorencito, 800-900 m, LN 244500-471500, October 20, 2001 (Rowell CHF), specimen no. 2001.094 (INBC); San Ramón, N. of R. Cataratas on road to S. Lorenzo, LN 244750-477000, Sep 8, 1976 (Rowell CHF), specimen no. 76116 (RC); Sector Colonia Palmarena, 700 m, LN 245900-475900, April 15, 1995 (G. Carballo), specimen no. 2 213249 (INBC); Cartago; Orosi LN 197750 552350, no data (UMMZ); Turrialba, grounds of CATIE, forested river gorge, LN 208500-575200, February 17, 1973 (Rowell CHF), (RC).

Guanacaste

Cerro El Hacha, 300m, P.N. Guanacaste, LN 329200-368000, May 15, 1988 (Espinoza M), specimen no. 0 661625 (INBC); Est. Pitilla, 7 km S. of Sa. Cecilia, 700 m, LN 330200-380400, May 15, 1990 (Curso Parataxonomos II), specimen no. 0 241812 (INBC); Tierras Morenas, Bajo Los Cartagos, R. S. Lorenzo, 1050m, LN 287800-427600, April 14, 1991 (Celso A), specimen no. 443744 (INBC); V. Tenorio, nr. summit of rd. from Tierras Morenas to Bajo Los Cartagos, LN 287250-426500, July 21, 1991 (Rowell CHF Elsner N), specimen no. 91094 (RC).

Heredia

Sarapiquí, Camp 700 m (former Finca A. Casante), LN 253600-527800, Apr 5, 1986 (Rowell CHF), specimen no. 86041 (RC); Sarapiquí, Cantarrana-Camp 700 m, LN 261500-531400, Apr 1, 1986 (Rowell CHF), specimen no. 86467 (RC); Cantarrana-Queb. Negra LN 261000-531400, Apr 3, 1986 (Rowell CHF), specimen no. 86473 (RC); Sarapiquí, Chilamate, Finca Selva Verde, 100 m, LN 269500-528500, July 16, 1991 (Rowell CHF) (RC); La Palma, 1500 m, LN 225600-537750, no other data (Valerio M) (ANSP); Sarapiquí, La Virgen, LN 264600-521500, April 24, 1993 (Ortiz M), specimen no. 1 677376 (INBC); Sarapiquí, Puerto Viejo, Finca La Selva, 40 m, LN 268800-535300, March 27, 1986 (Rowell CHF), specimen no. 86042 (RC); Sarapiquí, Finca Tirimbina, LN 264650-524550, February 19, 1973 (Rowell CHF), specimen no. 73047 (RC); Sarapiquí, Sendero Est. Magsasay a R. Sardinalito, 150-350 m, LN 261500-531000, January 15, 1991 (Fernandez A), specimen no. 1 607013 (INBC).

Limón

Guápiles, La Emilia, 1000', LN 243800-559900, (Rehn JAG) (ANSP); La Lola, 0.5 km W of Madre de Dios, LN 230770-602230, Oct 5, 1961 (Hubbell TH Cantrall I Cohn E) (UMMZ); P.N. Tortuguero, Cuatro Esquinas, LN 285000-588000, Apr 15, 1989 (Aguilar R Solano J), specimen no. 0 084461 (INBC); Pococí, Cariari, Finca La Suerte, 40-50 m, LN 269300-558700, March 25, 1997 (Zumbado M Chacón IA), specimen no. 2 566313 (INBC); Río Sardinas, R.N.F.S. Barra del Colorado, 10 m, LN 291500-564700, November 11, 1993 (Araya F), specimen no. 1 169996 (INBC); Río Toro Amarillo, 10 km LN of Guápiles, S of Quebrada Grande on trail to S. Valentino, LN 234000-558400, Sep 10, 1993 (Rowell CHF Tucker D) (RC); Río Toro Amarillo, 7 km N of Guápiles, 0.5 km N of Quebrada Grande, LN 237300-558100, July 14, 1991 (Rowell CHF Elsner N) (RC); Siquirres, LN 231400-590600, December 5, 1936 (Dodge CW) (MZHU).

S. José

Carrillo, LN 236000-542000 (ANSP); P.N. Braulio-Carrillo, waterfall loop trail, 850 m, LN 235000-540500-July 13, 1991 (Rowell CHF Elsner N) (RC).

NICARAGUA

Atlántico Sur: El Recreo, Zelaya, 30 m, 12° 10' N 84° 19' W, Oct 15, 1984 (Amédégnato C Poulain S) (MNHN).

Microtylopteryx hebardii nigrigena

PANAMA

Colón: Gatún, Tres Ríos Plantation, 9° 20' N 79° 55' W, March 15, 1930 (Zschokke TO) (CAS).

Coclé: Cerro Copé (P.N. Omar Torrijos), El Palmarazo, 8° 44' 80° 38', 27.08.2001 (Gonzalez P), specimen no. 2001.281 (GBFM).

M. fusiformis fusiformis.

COSTA RICA

Alajuela:

Dos Rios, Fca S. Gabriel, LN318800-383500, May 15, 1990 (Parataxonomos II Curso) specimen no. 0 644822 (INBC); La Libertad, in valley of R. Caño Negro, between PN Rincón de la Vieja and Piedras Blancas, 400-500 m, LN311000-402500, July 21, 1980 (Rowell CHF Rowell-Rahier M Hyde C) specimen no. 80725 (RC); Laguna Hule, 780-730 m, LN253900-513700, July 16, 1991 (Rowell CHF) (larva); Monteverde: path to Peñas Blancas, LN253300-450800, September 12, 1993 (Rowell CHF Tucker D) (RC); nr. Virgen del Socorro, Sarapiquí, 1000-800 m, LN248800-517500, April 23, 1986 (Rowell CHF), specimen no. 86034 (RC); R.B. San Ramón, Río San Lorencito, 1130 m, LN243900-471000, October 21, 2001 (Rowell CHF) (MUCR); San Carlos, LN272680-485630, (no other data) (MUCR); San Ramón, 10 km N on road to San Lorenzo, Queb. Azul del R. Balsa, 900 m, LN241750-480500, September 8, 1976 (Rowell CHF) specimen no. 76113 (RC); Sarapiquí, Cinchona, waterfall Río La Paz, 1470 m, LN243400-518600, October 15, 2001 (Rowell CHF) specimen no. 2001.031 (INBC).

Cartago:

Bajo Pacuare, 580-700 m, LN207400-589500, July 7, 1980 (Rowell CHF Rowell-Rahier M Hyde C) specimen no. 80197a (RC); Below pass between V. Irazu and V. Turrialba, S. side, 1900-2000m, LN217000-562500, July 6, 1980 (Rowell CHF Rowell-Rahier M Hyde C) (RC); Chitaria, 650 m, LN213300-581000, January, 1929 (Valerio M) (ANSP); Grano de Oro, 1120 m, Chirripó, Turrialba, LN291500-564700, September 15, 1992 (Campos P), specimen no. 935826 (INBC); Juan Viñas, LN208700-564300, March 1902 (Bruner L) (UMMZ); Navarro, N. foot of Candelaria Mts, 3800-3950', LN199600-549600, July 24, 1927 (Lankester CH Rehn JAG) (ANSP); Orosi, Río Macho, LN193000-553000, January 20, 1978 (Rowell CHF) specimen no. 78055 (RC); P.N. Tapantí, Rancho Negro, 1735 m, LN213300-581000, 7 October 1999 (Rowell CHF) specimen no. 99356 (INBC); Pacayas, SE slopes of Volcán Irazú, 6250', LN199600-549600, September 6, 1923 (Lankester CH Rehn JAG) (ANSP); Pejivalle, 2100', LN243800-559900, August 12, 1927 (Rehn JAG); Sa. Cruz, crossing of R. Aquiares & rd., 0.7 km NW of church, 1475 m, LN216900-565000, July 6, 1980 (Rowell CHF Rowell-Rahier M Hyde C) specimen no. 80723 (RC); Tapantí, 0-1 km past entrance to reserve, LN194000-559800, August 20, 1997 (Rowell CHF Singh I), specimen no. 97121 (INBC); Purasil, Quebrada Perla, LN193750-556800, August 14, 1979 (Rowell CHF & Rowell-Rahier M), specimen no. 79068 (RC); Tres Ríos, Cerro la Carpintera, 1500-1650 m, LN208300-538000, September 21, 1993 (Rowell CHF), specimen no. 93309 (RC); La Carpintera, Candelaria Mountains, 5100-6100', LN190000-507000, 4 September 1923 (Lankester CH Rehn JAG) (ANSP); Turrialba, LN210000-571000, (no data) (MUCR); Turrialba, LN208500-575200, April 17, 1957 (Shepefelt RD) specimen no. RDSS7-77 (USNMNH).

Guanacaste:

Cerro El Hacha, 300 m, P.N. Guanacaste, LN329200-368000, May 15, 1988 (Espinoza M) specimen no. 0 094321 (INBC); Est. Pitilla, 7 km S. of Sa. Cecilia, 700 m, LN330200-380400, Apr 10, 1992 (Taylor K) specimen no. 0 505703 (INBC); P.N. Guanacaste, S.E. slope of Volcán Cacao, 1040 m, LN323300-375300, July 31, 1987 (Braker HE), specimen no. 87007 (RC); Volcán Tenorio, nr. summit of rd. from Tierras Morenas to Bajo Los Cartagos, 1040 m, LN287250-426500, July 21, 1991 (Rowell CHF Elsner N) specimen no. 91095 (RC).

Heredia:

5 km. S of Los Cartagos (crossing of Rta 9 & R. Tabor), 1750 m, LN232730-518480, 21 June 1980 (Rowell CHF Rowell-Rahier M Hyde C) (RC); Sarapiquí, between Camp 1500 m. and Camp 2060 m, 1850 m, LN245000-526300, 12 April 1986 (Rowell CHF), specimen no. 86490 (RC); Sarapiquí, Camp 1500 m, LN245800-527200, Apr 11, 1986 (Rowell CHF) (RC); Sarapiquí, Camp 700 m. (former Finca A. Casante), LN253600-527800, April 5, 1986 (Rowell CHF), specimen no. 86475 (RC); Sarapiquí, Cantarrana, 380 m, LN261500-531400, Apr 1, 1986 (Rowell CHF), specimen no. 86466 (RC); Sarapiquí, between Cantarrana and Camp 700 m, LN261500-531400, 4 April 1986 (Rowell CHF) (RC); Est. El Ceibo, P.N. Braulio Carrillo, 500m, LN236000-542000, January 15, 1990 (C. Chaves), specimen no. 0 201846 (INBC); La Selva to Cantarrana road, LN268800-535300, 31 March 1986 (Rowell CHF) (RC); Sarapiquí, Puerto Viejo, Finca La Selva, 40 m, LN268800-535300, 30 March 1986 (Rowell CHF), specimen no. 86458 (RC); San Rafael de Vara Blanca, 1800-2000 m, LN239800-524200, 18 April 1986 (Rowell CHF Braker HE) specimen no. 86496 (RC); Sarapiquí, Camp 960 m (ridge between R. Peje & R. Sardinalito), LN250650-527900, Apr 9, 1986 (Rowell CHF) specimen no. 86486 (RC); Volcán Barba; 4 km. N. of Chompipe, 2300 m, LN233500-529500, September 9, 1976 (Rowell CHF), specimen no. 76108 (RC).

Limón:

3 km N. of Carrillo, Finca El Tapir, 550 m, LN236000-542000, July 14, 1991 (Rowell CHF Elsner N), specimen no. 91040 (RC); Guácimo, 600', LN244000-570000, June 7, 1909 (Calvert P) (ANSP); Guápiles, LN243800-559900, November 26, 1903 (Carriker JA) (ANSP); Río Bananito, 10 km N of Progreso, LN203000-640600, August 27, 1997 (Rowell CHF Singh I) specimen no. 2510506 (INBC); Río Toro Amarillo, 10 km S of Guápiles, S of Quebrada Grande, LN234000-558400, September 10, 1993 (Rowell CHF Tucker D) (INBC); Río Toro Amarillo, 1000', LN243300-556400, August 19, 1923 (Rehn JAG) (ANSP); Río Toro Amarillo, 7 km. N of Guápiles, 0.5 km N of Quebrada Grande, LN237300-558100, July 14, 1991 (Rowell CHF Elsner N) specimen no. 91045 (RC); Río Toro Amarillo, crossing with rd. from Guápiles, 305 m, LN243300-556400, July 9, 1980 (Rowell CHF Rowell-Rahier M Hyde C), specimen no. 80199a (RC); Siquirres, LN231400-590600, September 16, 1927 (Rehn JAG) (ANSP); Suretka Trail, between Sixaola and Valle de la Estrella, LN184000-650000, May 19, 1924 (Bradley JC) (ANSP); Valle de la Estrella, Concepción, 3 km SW, 1 km beyond R. Cerere, LN188000-642000, August 18, 1979 (Rowell CHF Rowell-Rahier M), specimen no. 79070 (RC); Valle de la Estrella, N end of Suretka Trail, along Duroy River, LN184000-650000, October 9, 1927 (Rehn JAG) (ANSP); Valle de la Estrella, Progreso, Finca Cantón, 300 m, LN192300-641000, June 27, 1980 (Rowell CHF Rowell-Rahier M Hyde C),

specimen no. 80715 (RC); Margarita, trail up Fila, 9.4 km after Bribri on rd. to Sixaola, 100 m, LS395500-598500, July 3, 1980 (Rowell CHF) (RC); Suretka, Sixaola Valley, LS392150-579500, April 4, 1924 (Bradley JC) (ANSP); 3 km. SW of Home Creek, 80 m, LS398800-594100, July 2, 1980 (Rowell CHF Rowell-Rahier M Hyde C) specimen no. 27161 (RC); 7 km N. of Suretka, 230 m, LS395450-583780, September 21, 1983 (Rowell CHF) (RC); Bribri, LS397200-591810, July 2, 1980 (Rowell CHF Rowell-Rahier M Hyde C) specimen no. 80722 (RC); Cerro Uatsi, above Bribri, 600 m, S396900-579600, August 24, 1997 (Rowell CHF Singh I) specimen no. 97196 (INBC); Est. Miramar, 500m, Res. Biol. Hitoy Cerere, LS398100-572800, August 25, 1992 (G. Garballo) specimen no. 0 857346 (INBC).

Puntarenas:

Est. La Casona, Res. Biol. Monteverde, 1520m, LN253250-449700, 15 December 1990 (N. Obando), specimen no. 0 664849 (INBC); Monteverde, Campbell's Bull Park, LN253500-448400, March 15, 1973 (Rowell CHF) specimen no. 73045 (RC); Monteverde, Refugio El Valle, 1525 m, LN254500-450500, July 17, 1980 (Rowell CHF Rowell-Rahier Hyde C) (RC); Monteverde, Sendero Nuboso, 1480-1520 m, LN253500-449400, July 14, 1980 (Rowell CHF Rowell-Rahier Hyde C) (RC); Monteverde, trail to La Ventana, LN253600-449500, September 12, 1993 (Rowell CHF Tucker D) (RC); P.N. Carara, Sendero de los Enterrados, 450-530 m, LN194000-477000, July 27, 1980 (Rowell, CHF and Rowell-Rahier M) (RC); Sonador, Finca Longo Mai, 700 m, LS357500-520500, August 22, 1995 (Rowell CHF Meier V), specimen no. 95321 (RC); Potrero Grande, Tres Colinas, 1945-2150 m, S342100-565600, September 12, 1995 (Rowell CHF Meier V) specimen no. 95537 (RC); Río Claro, Linda Vista above Bajo Bonito, 730-1000 m, LS299600-567300, August 31, 1995 (Rowell CHF Meier V) specimen no. 95433 (RC); S. Vito de Jaba, Fila Cruces, 8 km N of Concepción, 1400-1500 m, LS304500-572000, September 25, 1993 (Rowell CHF) (RC); S. Vito de Jaba, Finca Las Cruces, 1100 m, LS304500-577500, August 7, 1980 (Rowell CHF & Rowell-Rahier M) specimen no. 80366 (RC); San Vito de Jaba, Fila Cruces, above R. Chico, 1430 m, LS305900-569130, August 9, 1980 (Rowell CHF) specimen no. 80714 (RC); San Vito de Jaba, Fila Cruces, Finca Ilana, above R. Claro, 1280-1430 m, LS304500-570100, August 25, 1995 (Rowell CHF Meier V) (RC); Las Alturas, 1600 m, LS323400-591300, September 5, 1995 (Rowell CHF Meier V) specimen no. 95482 (RC); Las Alturas, above Tajo Buena Vista, 1700 m, LS324500-590500, Apr 1, 1980 (DeVriess P) specimen no. 80726 (RC); Las Alturas, Echandi trail, 1755 m, LS325500-591300, September 6, 1995 (Rowell CHF Meier V), specimen no. 95497 (RC); Altamira, above Finca Colorado, 1450 m, LS331400-571900, June 4, 2000 (Rowell CHF) specimen no. 2000.014 (RC); Sendero a Cerro Pittier, 1800-2100 m, LS331800-577400, February 28, 1995 (Zumbado MA) specimen no. 2 350793 (INBC); Osa Peninsula, Rincón de Osa, LS 294100-517800, January 1965 (Roberts HR) (ANSP).

S. José:

4 km from S. Jerónimo towards Alta la Palma on Rta 220, 1580 m, LN223950-537570, Apr 22, 1986 (Rowell CHF) (RC); Alto la Palma to Bajo La Hondura, 1520-900 m, LN226500-537800, July 31, 1991 (Rowell CHF Elsner N) specimen no. 91209 (RC); Between Cascajal and Tierras Morenas, 1600-1700 m, LN224000-543400, September 18, 1993 (Rowell CHF Tucker D), specimen no. 93251 (RC); Carrillo, LN236000-542000, no other data (ANSP); Hca Tiquirres, 1370 m, LN190400-515400, October 13, 2001 (Rowell CHF) specimen no. 2001.029 (RC); La Palma, between Volcánes Irazu and Barba, 5000 ft, LN225600-537750, September 1, 1927 (Tristan JF Rehn JAG) (ANSP); Monte Redondo, LN197000-522550, March 15, 1902 (L. Bruner) (MHNG); Moravia (= S. Vincente), LN216300-531000, May 30, 1976 (Solarno, G.) (MUCR); San José (ciudad), LN213400-530850, March 29, 1902 (Bruner L) (ANSP); Alto la Palma, 1655 m, LN225600-537750, Apr 22, 1986 (Rowell CHF) specimen no. 86036 (RC); Valle de El General, R. Unión, 3 km N. of Zapotal, 1345 m, LS367600-517800, Juni 7, 2000 (Rowell CHF) specimen no. 2000.105 (RC); Pozo Azul de Pirris, 325-550 ft, LS400200-431200, August 5, 1903 (MZHU); Road nr. crest of Fila Tinamastes, 900 m, LS362800-488200, June 7, 2000 (Rowell CHF), specimen no. 2000.071 (RC). Rta 2, km 113 (7 km uphill from R. Paynor), 1900 m, LS380300-498100, September 18, 1995 (Rowell CHF Meier V) (RC); Rta 2, km 117-118 (2-3 km uphill from R. Paynor), 1600-1695, LS381200-497600, September 18, 1995 (Rowell CHF Meier V) specimen no. 95632 (RC); Cerro Nara, NE of Quépos, S382300-462000, July 16, 1975 (Hanson WJ) (EMUS).

MEXICO

Chiapas: Selva Lacandona, Chajul, 16°04'N 90°55'W, November 10, 1986 (Amédégnato C Poulain S) (MNHN).

NICARAGUA

Matagalpa: Matagalpa, Hca. La Cumplida, ca 4000', 13°N 85°50'W, July 16, 1957 (A. Starrett and party) (UMMZ).

Atlántico Sur: El Recreo, Zelaya, 30 m. 12°10'N 84°19'W, October 15, 1984 (Amedegnato C Poulain S) (MNHN).

PANAMA

Bocas del Toro:

10 km. W. on road from Punta Peña to Almirante, 9°00'N 82°20'W, September 21, 1999 (Rowell CHF Bentos A) (RC); Isla Colón, 9°25'N 82°20'W, July 24, 1999 (Cambra R) specimen no. 2001.291 (GBFM); Rambala, 4 km. on trail to Queb. Platanarito, 150 m. 8°50'N, 82°05'W, September 20, 1999 (Rowell CHF Bentos A) (RC); Changuinola District; United Fruit Co., 9°25'N 82°33'W, 10.10.1925 (Walker FW) (UMMZ); Guabita District, United Fruit Co., 9°30', 82°37'W, October 30, 1925 (Walker FW) (UMMZ); Las Delicias, United Fruit Co, October 1, 1925 (Walker FW) (UMMZ); Wekso, Region Teribé, Parque Internacional de la Amistad. 9°22'N 82°45', October 20, 1999 (De Gracia L Santos A) specimen no. 2001292 (GBFM).

Chiriquí:

25.2 km E of Río Sereno, 8°48'N, 82°45'W, April 24, 1976 (Rentz DC Carter MS Mullinex CL) (CAS); El Volcán, Bambito, 8°50'N, 82°40'W, November 3, 1978 (Espinoza D) specimen no. 99267 (GBFM); El Volcán, Cerro Punta, 5600', 8°52'N, 82°35'W, February 15, 1937 (Bishop DW) (ANSP); Parque Internacional La Amistad, Jurutungu, 1800 m, November 1, 1994 (Arjona R) specimen no. 99268 (GBFM); Valle de las Minas, 3 km N. on rd. to Chiriquí Grande, 8°25'N 82°42'W, September 25, 1997 (Rowell CHF Bentos A) specimen no. 97516 (STRI).

Veraguas:

Santa Fé, Alto la Piedra, 8°33'N 81°08'W, November 16, 1999 (De Gracia L Santos A Gonzalez P) specimen no. 99517 (GBFM).

M. fusiformis chiapensis.

GUATEMALA

Chimaltenango: Acatenango, 14°33'N 90°57'W, 15 May 1948 (Dalmat HT) (USNMNH); Yepocapa, 14°30'N, 90°57'W, August 15, 1948 (Dalmat HT) (USNMNH).

MEXICO

Chiapas: La Esperanza, 17°30'N 92°40'W, 15 October 1939 (C. Bolívar and D. Peláez) (MNHN); Sierra Madre del Sur, Vergel, 800 m, 16°07'N, 93°05'W, 12 June 1935 (Dampf A) (ANSP).

M. fusiformis fastigiata.

PANAMA

Bocas del Toro: 1-3 km past watershed on new road from Fortuna to Chiriquí Grande, 8°46'39"N, 82°12'23"W, September 23, 1997 (Rowell CHF Bentos A) specimen no. 97439 (ANSP); Quebrada Felix, 2 km NW of summit of rd. to Chiriquí Grande, 8°46'39"N 82°12'23"W, September 26, 1997 (Rowell CHF Bentos A) specimen no. 97537 (RC).

M. fusiformis worthi.

HONDURAS

Olancho: P.N. La Muralla, 1480 m, 15°05'49"N, 86°44'17"W, 5 July 2002 (Yanega D) specimen no. UCR71245 (UCR).

Atlantida: Tela, United Fruit Co., Dakota Farm, 15°47'N, 87°55'W, 17. May 1923 (T.H. Hubbell) (UMMZ); El Progreso, United Fruit Co., Farm III, 15°24'N 87°50'W, 19 May 1923 (T.H. Hubbell) (UMMZ); Lancetilla, near Tela, 15°45'N 87°28'W, 3 Sept 1930 (ANSP Honduras Expdtn) (ANSP).