

New Data on the Wing Morphology of the Cretaceous Sphecomyrminae Ants (Hymenoptera: Formicidae)

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Abstract—Previously unknown features of the wings of the Cretaceous Sphecomyrminae (Formicoidea) are described. The possibility of venation character distortion in inclusions is shown experimentally and should be taken into account in descriptions of fossil materials. In the light of the data obtained, principles for describing wing venation of ants and its variation are proposed. Problems of ant wing nomenclature are discussed.

Keywords: Formicidae, Sphecomyrminae, wing morphology.

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INTRODUCTION

The discovery of Late Cretaceous formicoids in amber from New Jersey, the United States (Wilson et al., 1967) was an important event for the study of the early evolution of ants. The specimens described, wingless females, were placed in a separate subfamily, Sphecomyrminae. *Sphecomyrmra freyi* (Wilson et Brown) had features that made it similar to scolioid wasps (bidentate mandibles, relatively short scape) and ants (metapleural glands, petiole narrowly attached to abdomen). Although some authors placed Sphecomyrminae at the base of the phylogenetic tree of ants, i.e., considered them to be an ancestral group to recent ant subfamilies (Taylor, 1978), the opinion that the subfamily Sphecomyrminae, being a member of Formicidae, is a blind branch of formicoids currently appears better justified (Dlussky, 1987; Grimaldi et al. 1997; Engel and Grimaldi, 2005). To date, 13 species of Sphecomyrminae are known, as well as three males that belong to unidentified species and/or genera, from the period 100 to 75 million years ago, from Cretaceous ambers of Canada, United States (New Jersey), France, Burma, and Taimyr Peninsula in Russia (Dlussky, 1975, 1987, 1996; Wilson, 1985; Grimaldi et al. 1997; Engel and Grimaldi, 2005; Perrihot et al., 2007). These records are inclusions of workers (14 specimens), winged males (12 specimens), and one winged female; only the female is associated with workers (found in the same piece of amber). It is known that males are little used in modern ant taxonomy, and studies of their morphology, with the exception of genitalia, are lacking. In this situation, describing species from isolated males is difficult, and it is impossible to associate previously described males with workers or females. Wings, how-

ever, are the structure that can be used as the basis for associating males and winged females. It was shown in a number of studies that wing venation not only is a good marker of subfamily, but also displays species-specific traits identical in individuals of both sexes (Dlussky, 1981, Reyes Lopez and Porras Castillo, 1984; Perfilieva, 2007, 2008). At the same time, the information provided in paleontological studies in diagnoses of taxa is usually insufficient for comparative analysis. The purpose of this study is to analyze the wings of Sphecomyrminae and describe them as thoroughly as possible. With this purpose, the following tasks have been set: to study the available Sphecomyrminae inclusions and descriptions of Sphecomyrminae wings provided in the literature; to determine the difficulties in descriptions and reconstructions of wings; and to propose means to overcome these difficulties.

MATERIALS AND METHODS

In this study, the wings of Sphecomyrminae stored in Borissiak Paleontological Institute, Russian Academy of Sciences (PIN), are discussed: *Baikuris mandibularis* (Dlussky), holotype, no. 3730/5 (male), and paratype, no. 3730/6; *Baikuris mirabilis* (Dlussky), holotype, no. 3730/8, Lake Taimyr, Baikura-Neru Bay, late Upper Cretaceous; *Dlusskyidris zherichini* (Dlussky), holotype, no. 3311/364, and paratype, no. 3311/366, Yantardakh, Taimyr Peninsula, Khetana Formation, Upper Cretaceous, Santonian. The specimens were studied using light binocular microscope Leica Z9.5. The sample was attached to the cover slip with a drop of sugar syrup, and the slip was fixed on a piece of plasticine, which allowed easily changing the viewpoint. Based on photographs taken with different

depth of focus using a Nicon D70 digital camera, an image with greater depth of focus was obtained in the program Helicon Focus 4.

The influence of the optic medium on determining the presence of spectral veins was studied in media with similar refractive index, glycerol (liquid) and epoxy resin (solidified), in transmitted and reflected light, using wings of recent ants comparable in size to Sphaeromyrmicinae (*Myrmica* sp., *Tetramorium* sp., etc.).

RESULTS AND DISCUSSION

The accuracy and completeness of inclusion descriptions are influenced by a number of factors. Some are related to the paleontological material itself; some, to description methods. For instance, obstacles to describing the morphology of insects in amber include fissures in samples, presence of other inclusions, "milky" pellicle, and inconvenient position of specimens. Difficulties of this sort are usually discussed at the author's discretion. In such cases, methods of graphic smoothing and combined reconstruction are usually used (Baroni Urbani, 1980; Dlussky, 1988). These methods are based on the reconstruction of the individual from preserved symmetrical parts and/or preserved parts of different specimens (paratypes). Reconstruction results in a combined specimen in a position convenient for description. The method is described in studies briefly, if at all, and sometimes supplemented with photographs of inclusions. The development of new methods of study, such as X-ray micrography and tomography (Tafforeau et al., 2006; Lak et al., 2008; Sutton, 2008; etc.) provides unique opportunities for work in this field. Descriptions are sometimes hindered by plastic deformation of fossil resins. Such cases require a different approach. This problem was addressed in a study of ants from Sakhalin amber (Dlussky, 1988). To reconstruct the natural position and appearance of structures, data on the functional morphology of recent ants, as well as assessment and graphic "correction" of plastic deformations in the resin that contains inclusions were used. In this approach, the methods are described in more detail. Thus, estimation of the accuracy of reconstruction is possible in cases where peculiar features of the inclusion (position, alien inclusions) and reconstruction methods are described, and good quality photographs are given. In all these cases, the final result of reconstruction, figure and description of characters, depends on two factors: the investigator's experience and the standards developed for describing morphology. The importance of the latter factor for the accuracy of description is considerable. Each researcher intuitively understands the existence of difficulties of this kind; however, he or she solves this problem according to his or her own experience within the limits set by existing standards. Studying wing venation, the author has encountered the problem of insufficient precision and lack of details in figured

wings of both fossil and recent ants. This situation made it impossible to compare wings described in different publications. The author believes that the main reasons of this situation are as follows:

(1) Different authors use different nomenclatures. In most studies, the somewhat outdated Brown's nomenclature (Brown and Nutting, 1950) is used; some authors use their own (Perrichot et al., 2007) or mixed nomenclature (Grimaldi et al., 1997); in Russian publications, Rasnitsyn's nomenclature (1980) is used.

(2) Different authors select different characters (sometimes cells, sometime veins, and often not the same).

(3) Descriptions (reconstruction) of the wings of inclusions often take no account of deformations of the wing, not only those caused by optic effects (which are, of course, hard to take into account), but also those caused by the position and flexure of the wing.

Brown's venation nomenclature (Brown and Nutting, 1950) is accepted by many myrmecologists. However, the study of Rasnitsyn (1980), who specified and corrected the origin and names of hymenopteran wing veins, showed the necessity to review this nomenclature. In this study, a nomenclature of ant wing venation based on Rasnitsyn's work is proposed (Fig. 1). A developed nomenclature is a necessary condition for standardization of wing character description, but this condition is not sufficient. After this, it is required to designate particular characters and their states. Such attempts have been made by several authors, with different degrees of success. In the same work by Brown and Nutting (1950), it is indicated that not only cells, but also segments of veins should be described. Listing all such segments is inefficient, and since these authors have not indicated which segments and variations are important (with the exception of the reduction of some segments), these recommendations cannot be considered felicitous. Another author provided a classification of wing veins based on the stage of their reduction, which manifests itself in changes of vein morphology (*tubular*, *nebulous*, and *spectral* stages) (Mason, 1986). Mason proposed a particular method for figuring not only the stages of vein reduction, but also fold lines, wing flexions. In his opinion, this would help to avoid loss of taxonomic and phylogenetic information. The author believes that, while such detailed figuring of wings is, of course, preferable, it will hardly gain much support because of the amount of required work. The author would also like to emphasize two important points that should be taken into account in descriptions. The first is the presence of spectral (non-pigmented, unsclerotized) veins. In recent members, such veins are almost invariably indicated as present, while, as shown by the author's experiment, in fossilized material (embedded in resins or sedimentary deposits) they would be invisible. Spectral veins 4M and 3Cu in *Myrmica* males are clearly visible in reflected light, but poorly discernible

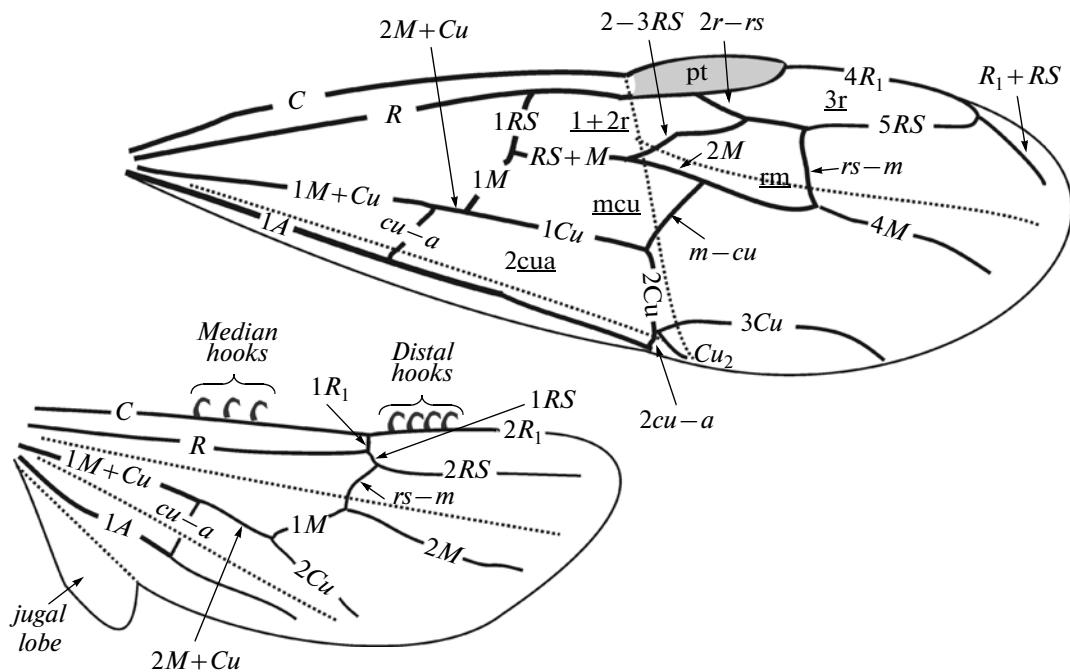


Fig. 1. Nomenclature of veins and other structures of ant fore- and hindwings. Cell names are underlined; vein names, italicized. In vein notation, number in front of letter is serial number of vein segment from wing base; plus sign (“+”) indicates fused veins; subscript shows vein branch (e.g., R_1 is anterior branch of radial vein). Dotted line shows position of functional folds and lines of wing flexion.

in transmitted light, in glycerol and in solidified epoxy resin (Pl. 6, figs. 1–5). Second, the distinction should be drawn between features determined by functional causes, such as vein fenestra, related to flexion lines, and features of different nature, but also important for diagnostics.

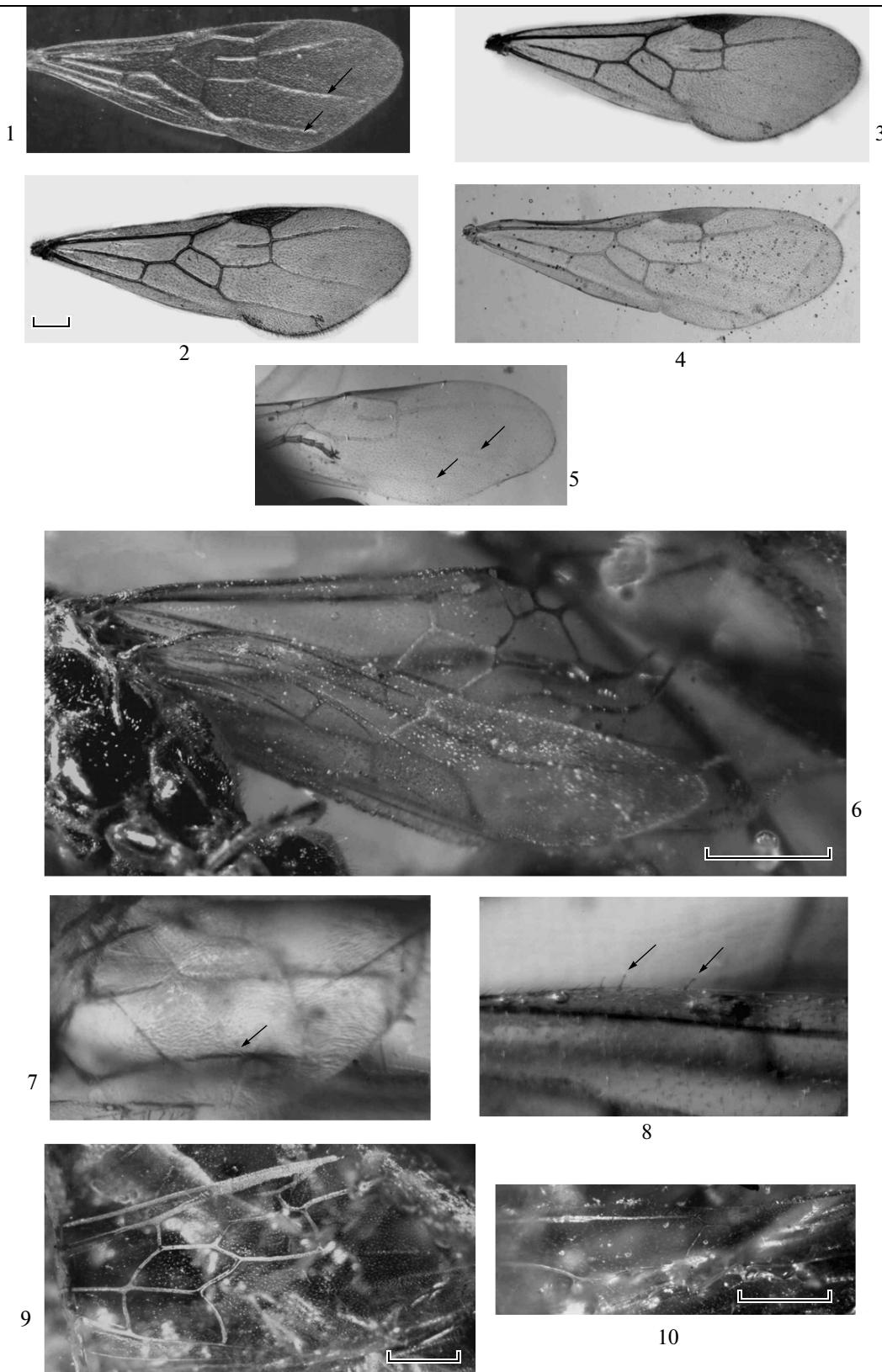
In descriptions of ant wing venation, the number of closed cells ($1r$ – $3r$, rm , mnu , $2cua$) is often given, but the shape of the cells is rarely characterized. Judging by the author's investigations, the following characters are important for characterizing closed cells: (1) number of “angles” in cells rm and mnu (the author proposes to use the term “angle” for every place where an external vein branches off; e.g., in *B. mirabilis* cell rm has six angles); (2) shape of cell mnu (trapeze or parallelogram): its shape is assessed from mutual incline (not from relative length) of m – cu and $1M$; (3) other peculiar features of cells should be indicated, if they exist (e.g., extremely long or short cell $3r$)—in other cases, the formula “without peculiar features” is acceptable. It is convenient to use for this purpose a system of venation types developed for ants, for instance that proposed by the author (Perfilieva, 2008) (Fig. 2), supplemented by a description of the characteristics recorded. The author's studies of the evolution of ant wing venation have shown that some segments of veins are important for phylogenetic studies (Perfilieva, 2008). Such characters include, in the forewing, the length and incline of segment $1RS$, vein $2r$ – rs , transverse vein m – cu , segment $2Cu$, presence

of veins $2cu$ – a and Cu_2 , length of segments $2M$ and $4RS$, position of vein cu – a relative to cell mnu and wing base, and presence of elongated segment R_1 + RS ; in the hindwing, length and ratio of seg-

	Reduction class				
	I	II	III	IV	V
Versions					

Fig. 2. Classification of forewing venation types in Formicidae. Class of reduction are consecutive transformations of venation from most complete (class I) to most reduced (class V). Variants correspond to venation variations at each stage of reduction.

Plate 6



ments 1RS, rs—m, 1M, 2M + Cu, as well as presence of secondary hamuli and jugal lobe.

Extremely little attention is paid to the third of the above causes of imprecision in wing descriptions. The author has almost never encountered remarks describing the position of the wing that may result in mistakes in any reconstructions. Such a description, however, would help to distinguish characters according to their degree of reconstruction reliability. For instance, the first reconstruction of *B. mandibularis* (Dlussky, 1987), due to folds in the wings of the inclusion, incorrectly represents the ratio and mutual position of areas 2r—rs, 4RS, and 2M in the forewing and 2M + Cu and 1M in the hindwing (Figs. 3a, 3b). In some cases, only drawings based on photographs, without reconstruction, are given. This is the case with the description of the female *Haidomyrmodes mammuthus* (Perrichout, Nel, Néraudeau, Lacau et Guyot) (MNHN ARC 50.2): the photograph of the inclusion shows that the wing is deformed, but the deformed areas are not indicated in the drawing, so that the drawing represents, in fact, the wing projection (Perrichot et al., 2007). Figures 3a—3c, showing drawings based on photographs and a reconstruction prepared taking into account the deformations, illustrate this problem. The reconstruction of specimen AMNH NJ—107 (Grimaldi et al., 1997) is a different case. The authors of this reconstruction indicate that the specimen has transverse m—cu and 3Cu in the forewing reduced (Fig. 4a); other characters of the wing are not discussed. At the same time, the original drawing distinctly shows a curve in the vein at the place where 2M transforms into 3M. This curve may result from intraspecific variation in the degree of this vein reduction. Such variation is often observed in sexual individuals of small-sized recent species (Perfilieva, 2000). There are data on recent ants (Perfilieva, 2008) which indicate that the existence of such a curve supports this assumption. But the other side of the cell, vein 1—2Cu, which also takes part in this process, looks unnatural: there is no curve, but neither is there distinct straightening of the vein, which takes place in cases where the loss of m—cu is secured by evolution. Precise reconstruction requires comparing the visible venation of forewings in different aspects of the specimen and recording the detailed venation of this area. Since wings are indistinct in the photograph, it is difficult to come to any conclusions about its wing. Such exam-

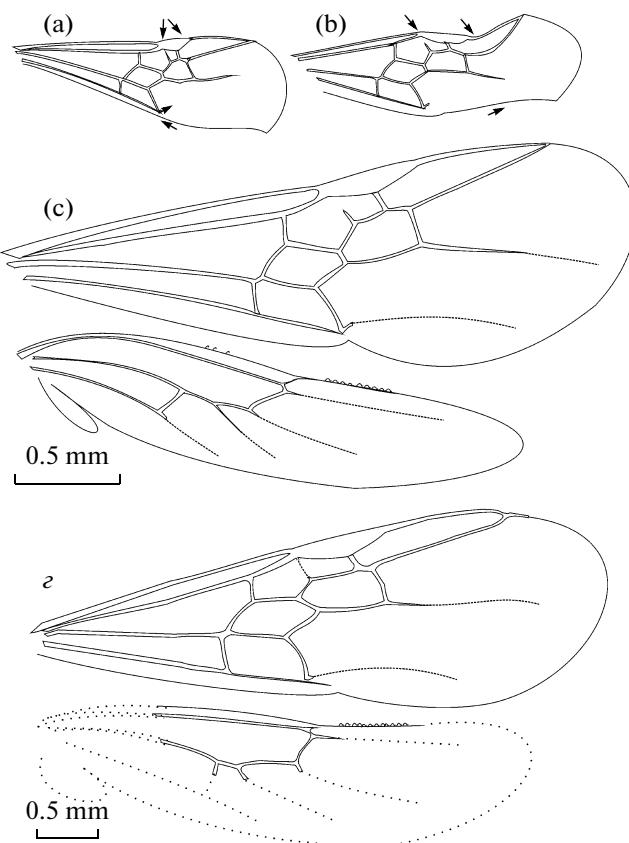


Fig. 3. Drawings based on photographs of (a) left and (b) right forewings of *Baikuris mandibularis* Dl., specimen no. 3730/5; reconstructions of wings of (c) *B. mandibularis* Dl. and (d) *B. mirabilis* Dl. Arrows indicate areas of wing deformation; dashed lines, spectral veins; dotted line in hindwing of *B. mirabilis*, completed missing details of venation.

ples are numerous—descriptions are detailed only in exceptional cases.

Sphecomyrminae wings available to the author are described below without these defects. The holotype of *B. mandibularis* is embedded in a piece of transparent reddish retinite (Pl. 6, figs. 6—8). The wings are clearly visible from the base to the apex of cell 3r. The forewing is about 3 mm long; the hindwing is about 2.4 mm long. The left hindwing is positioned in front (Fig. 3a). The hindwing is longitudinally folded along vein M + Cu, with its posterior part directed towards the center of the sample. The apex of the left forewing

Explanation of Plate 6

Figs. 1—5. Forewing of *Myrmica* sp. (1) in reflected light, (2) in a combination of transmitted and reflected light, (3) in transmitted light, (4) in a combination of transmitted and reflected light in glycerol, and (5) in a combination of transmitted and reflected light in epoxy resin.

Figs. 6—8. *Baikuris mandibularis* Dl.: (6) holotype, no. 3730/5; (7) distal portion of forewing, paratype, no. 3730/6; (8) secondary hamuli of forewing, holotype, no. 3730/5.

Figs. 9 and 10. *Baikuris mirabilis* Dl., holotype, no. 3730/8: (9) forewing; (10) hindwing. Arrows indicate spectral veins (4M, 3Cu) in forewing and secondary hamuli in hindwing. Scale bar, 0.5 mm.

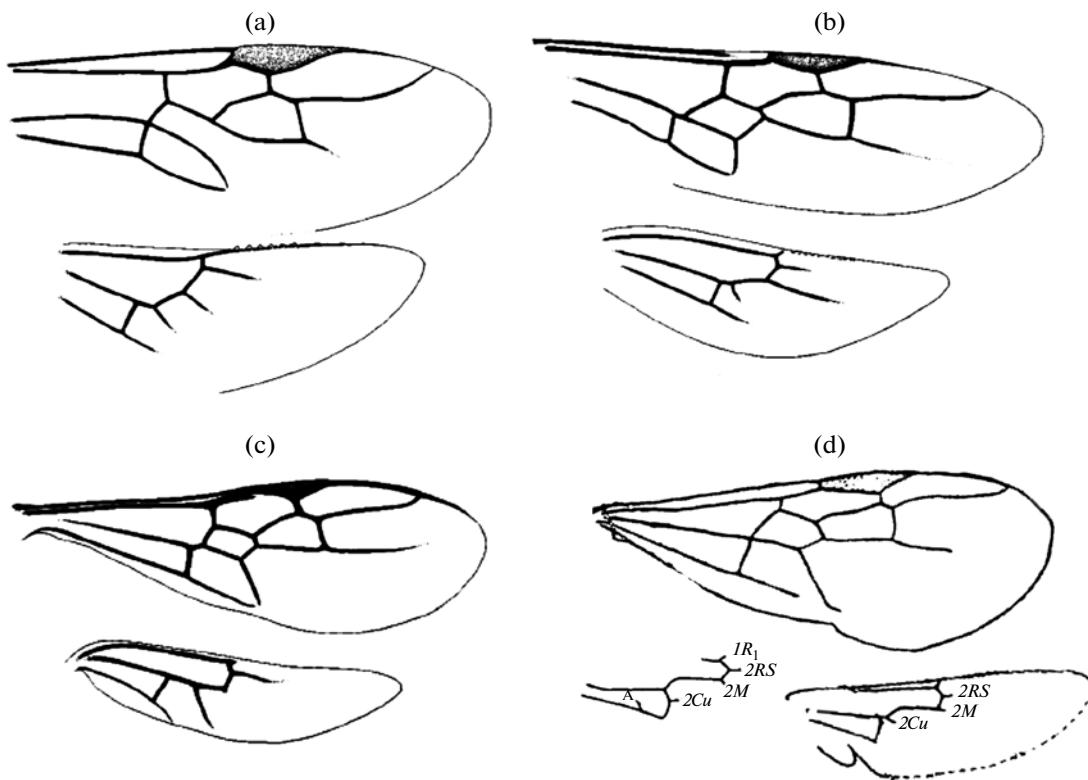


Fig. 4. Reconstructions of Sphecomyrminae wings from (a, b, c) Grimaldi et al. 1997 and (d) Dlussky, 1975: (a) male of unidentified genus, AMNH NJ-107; (b) *B. casei* Grimaldi, Agosti et Carpenter, AMNH 90bb; (c) *Sphecomyrma* (?), AMNH NJ-242; (d) *Dlusskyidris zherichini* Dl., no. 3311/364-366, forewing and two versions of hindwing.

is curved towards the surface of the sample from the transverse line between the base of pterostigma and the distal angle of cell *mcu*. The lower part of the forewing posterior to anal vein is curved anteriad. Details of the right forewing, transversely curved in the area of cell *3r*, are distinguishable (Fig. 3b). The venation of the forewing agrees with class Ia in the diagram (Fig. 2), with closed cells *3r* and *cua* (reconstruction shown in Fig. 3c). Cells *1r* and *2r* are divided by an incomplete but well-developed transverse vein *1r-rs*. Cell *3r* is without peculiar features, medium-sized, without segment *R₁ + RS*. Cell *rm* has six angles: segment *2M* is short (less than one-third of *RS + M*); areas *2RS*, *3RS*, and *4RS* are subequal in length. Segment *1RS* is perpendicular to *R*; *2r-rs* is vertical or slightly inclined towards the wing apex, without peculiar features. Vein *1r-rs* is sclerotized from cell *rm* approximately to the middle; the other half of the vein is most probably absent or spectral. Cell *mcu* has five angles. The anterior end of vein *m-cu* is inclined towards the wing apex and almost parallel to *1M*, so that cell *mcu* is parallelogram-shaped. Cell *mcu* reaches the level of the base of pterostigma. Cell *cua* is well-formed, subequal in area to cell *mcu*. Transverse *cu-a* is relatively long, shorter by about one-third than vein *m-cu*, positioned close to cell *mcu* and relatively far from the

wing base, so that $Icu_{1r} = 1.03-1.09$ and $Icu = 1.15-$

¹ Vein *2Cu* forms a distinct angle with vein *1Cu*, so that *2Cu* is almost parallel to *2cu-a*. Cell *cua* is parallelogram-shaped; vein *2Cu* is at most 1.5 times as long as *cu-a*; other veins of this area (*2cu-a*, *Cu₂*) are not distinguishable. Vein *3Cu* is spectral, clearly visible in the paratype (Pl. 6, fig. 7).

The hindwing has all transverse veins *2R₁*, *2M*, *2Cu*, and *2A*, but only their proximal parts are pigmented (Fig. 3c). Transverse vein *cu-a* is relatively long (subequal in length to *2M + Cu*), positioned distally: segment *1M + Cu* is at least 5 times as long as *2M + Cu*. Segment *1RS* is short and well developed. Segments *rs-m* and *1M* are of subequal length; *2M + Cu* is slightly shorter, but the internal angle between *rs-m* and *1M* is slightly greater than 90°, and the internal angle between *1M* and *2M + Cu* is almost 180°. The distal hamuli are at least nine in number; three secondary hamuli are visible (Pl. 6, fig. 8), but they are obviously greater in number. The jugal lobe is small. Frontal veins *C* and *2R₁* are not sclerotized.

The holotype of *Baikuris mirabilis* is embedded in a piece of transparent reddish retinite (Pl. 6, figs. 9, 10;

¹ $Icu = ([1M + Cu] + [2M + Cu]) / [1M + Cu]$; $Icu = ([2M + Cu] + 1Cu) / 1Cu$. From Dlussky (1981).

reconstruction in Fig. 3d). The forewings are positioned close to the surface. The apex of the right wing is clearly visible but curves towards the center of the sample; the wing darkens medially. The left forewing is lacking its base and apex, due to cleavage. The forewing is about 4.7 mm long; the hindwing is about 4 mm long. The forewing belongs to class Ia, with closed cells 3r and 2cua. The first and second radial cells are completely separated by complete, transverse vein 1r–rs. Transverse 1r–rs is narrow, visible only from some viewpoints. Cell 3r is medium-sized; a short segment of R₁ + RS is present along the wing margin. Cell mcu has five angles; length of segment 2M is approximately half as long as segment M + RS. Cell rm has six angles: segment 2M is long, approximately half as long as RS + M. The ratio between the lengths of segments 2RS, 3RS, and 4RS is approximately 2 : 3 : 1. Vein 2r–rs is vertical or slightly inclined towards the wing apex; angle between 1RS and R is somewhat smaller than right angle, without peculiar features. The anterior end of vein m–cu is inclined towards the wing apex; this vein is almost parallel to 1M (cell mcu is parallelogram-shaped). Cell mcu reaches the level of the base of pterostigma. Cell cua is well developed, subequal in area to cell mcu. Transverse vein cu–a is relatively long, slightly shorter than vein m–cu, positioned near cell mcu and relatively far from the wing base, so that Icu = 1.08–1.11 and Icu = 1.16–1.27. Vein 2Cu forms a distinct angle with 1Cu, so that 2Cu is almost parallel to 2cu–a. Cell 2cua is parallelogram-shaped; segment 2Cu is subequal in length to m–cu; other veins of this area (2cu–a, Cu₂) are indistinct. Vein 3Cu is spectral, clearly visible from some viewpoints. The hindwing is fragmented: the median part and the base are visible separately. All longitudinal veins 2R₁, 2M, 2Cu, and 2A are present, but only their proximal parts are sclerotized (Pl. 6, fig. 10; Fig. 3d). Transverse vein cu–a is probably relatively long, positioned distally: segment 1M + Cu is at least 6 times as long as 2M + Cu. Segment 1RS is short but well developed. Segment 1M is approximately 1.5 times as long as segment rs–m and 3 times as long as segment 2M + Cu; the internal angle between rs–m and 1M is slightly greater than 90°, and the angle between 1M and 2M + Cu is slightly smaller than 180°. The distal hamuli are at least 12 in number; fissures in the area of secondary hamuli make it impossible to determine whether they are present. The area of jugal lobe is incompletely visible; however, the presence of this lobe is obvious, judging by the wing outline. Veins C and 2R₁ are not sclerotized.

Unfortunately, details of the wing venation of *Dlusskyidris zherichini* are almost invisible under light microscope: storage of the specimens in castor oil has resulted in the disappearance of air cavities in the inclusion (the refractive index has changed); this has had especially regrettable effect on the visibility of wings. However, the study of negatives made at an

early stage of the study of these inclusions, and their comparison with details that can be distinguished at present in paratype no. 3311/366 have shown that the reconstruction of Dlussky (1975) is relatively correct. Nevertheless, in some negatives 3Cu is clearly visible in the forewing of the paratype, and two secondary hamuli are visible under the microscope in the hindwing.

The author has determined that in male wings of at least three Shecomyrinae species the distal segment of the cubital vein (3Cu) is not completely reduced and is represented by a spectral vein. In the light of the fact that spectral veins 3Cu are widespread among relatively small recent ants, this character cannot be considered a unique synapomorphy of Sphecomyrminae. In the male hindwings of *B. mirabilis* and *B. mandibularis*, as well as in *B. casei* (Grimaldi, Agosti et Carpenter) (AMNH 90bb), *Sphecomyrmia* (?) AMNH NJ-242 (from Grimaldi et al., 1997) (Fig. 4), and *Sphecomyrmia* (?) AMNH NJ-942 (description from Engel and Grimaldi, 2005), the angle between 2M + Cu and 1M is almost undeveloped. This character could be considered synapomorphic for the subfamily, if it were not for two reconstructions. According to Dlussky's reconstruction (1975), the hindwing venations of *D. zherichini* is similar to that in the wings of the more primitive Armaniidae. However, the figure shows that two different versions of venations were given (Fig. 4d). Another exception is the male hindwing of specimen AMNH NJ-107 (not identified by the authors of the genus), which, if the reconstruction (Grimaldi et al., 1997) is correct, is similar in the mutual position and ratio between segments rs–m and 1M to that of recent primitive ants (Fig. 4a). The possibility that this male does not belong to Sphecomyrminae cannot be excluded, but the question lies outside the scope of this study.

The jugal lobe has been found in three species of Sphecomyrminae (*B. mandibularis*, *B. mirabilis*, and *D. zherichini*), but its absence in other winged Sphecomyrminae cannot be considered proven, because this area of the wing is usually poorly visible in inclusions, and authors of descriptions provide no conclusions about its presence. The same is true of secondary hamuli, the presence of which the author has discovered in *B. mandibularis* and *D. zherichini*. Clear and reliable unique apomorphic characters for the entire subfamily could not be found based on the author's data and reconstructions by other authors, although similar features in the hindwings of Sphecomyrminae found by the author may prove to be apomorphic for a group of lower rank. In the forewing, the decrease in the length of 2M, compared to that in Armaniidae, with preserved distal position and incline of transverse m–cu, is, perhaps, the only character that can be currently considered a common advanced trait, since it is shown in all reconstructions of Sphecomyrinace wings, while in recent ants, with the exception of some

poneromorphs, decreased length of 2M is related to changes in incline and more proximal position of m–cu. The fact that in publications venation is not represented with sufficient detail and precision cannot be a reason to conclude with certainty that no other apomorphic characters will be found as a result of more thorough studies. Sphecomyrminae wings doubtlessly display forewing venation that is primitive compared to recent ants but have a number of advanced features compared to Armaniidae (for instance, the more proximal position of transverse veins rs–m and m–cu, reduced length of 2M). On the other hand, the hindwings of most Sphecomyrminae display apomorphic traits different from other formicoids.

CONCLUSIONS

The absence of sufficiently detailed and correct reconstructions of Sphecomyrminae wings is an obstacle in the way of determining the apomorphic characters of their venation. Apomorphic forewing venation traits relative to Armaniidae wings and unique apomorphic hindwing venation traits found in most members of the group have been determined in Sphecomyrminae. For a more complete and reliable description and reconstruction of ant wings, the following rules should be followed. A well-developed nomenclature should be used. Currently that is Brown's nomenclature (Brown and Nutting, 1950), or the more detailed nomenclature proposed in this study. As many as possible venation details should be represented. The character states of significant venation characters recognized in this study should be used. The presence of spectral veins, functional fenestra, and other peculiar features of the wings should be indicated. In the course of reconstruction in paleontological studies, the position of the wing and places of deformation that hinder or distort the reconstruction of the wing should be taken into account.

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