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Notes on the Morphology and Classification of the Sarcophagidae and Other Calyptrates (Diptera).

By WILLIAM L. DOWNES, JR.

INTRODUCTION

The application and correlation of recently discovered characters with others already in use in the Sarcophagidae clarify some problems of relationship among the major divisions of this family. The Agriini, including *Wohlfahrtia*, may be much more accurately defined, and may be shown to be very closely related to the Miltogramminae, but not so closely related to the Sarcophaginae with which they are often associated. Below tribal level relationships are still obscure, although certain natural groups are roughly recognizable. Published studies presenting more detailed phylogenetic systems for these lower levels can be shown to be untenable on the basis of recent information.

During the course of this study several important papers on the morphology of other Diptera were found to have direct bearing on the morphology of the Sarcophagidae with the result that some structures in this family (and other calyptrates) are now homologizable with structures of lower Diptera and, often, with those of other orders. Accordingly, several nomenclatorial changes are adopted in this paper. Such changes are not altogether welcome to some systematists; but, in view of the fact that many of these terms are already in use in several nematocerous families, it does not seem wise to prolong the use of a completely separate system of terminology as is now reserved for the higher Diptera.

Other terms new to the Sarcophagidae were necessitated by the application of characters which have not yet been used in the family. The value of such characters makes their introduction desirable, especially since there is at present an apparent paucity of modifications applicable to females. These characters are also offered to support the idea that the Sarcophagidae are not so devoid of external characters of phylogenetic significance as is sometimes thought; and further study is likely to result in the discovery of more usable modifications.

MORPHOLOGY

Adult—Thorax Proper (Figure 1)

Mesoepisternum The numerous similarities between the tabanid thorax and the calyptrate thorax are apparent; and, consequently,

the conclusions of Bonhag (1949) regarding many homologies of the thorax of *Tabanus* are applicable with little modification within the Calyptratae. The angled course of the mesopleural suture is easily established by means of a dissection, as is the location of the mesoanepisternal suture. Thus, the mesopleuron and sternopleuron of taxonomists are seen to be identical with the mesoanepisternum and mesokatepisternum, respectively. For descriptive purposes the sternopleural macrochaetae may be referred to as the katepisternals, since comparable areas do not occur on either the pro- or the metathorax.

Mesoepimeron, meron The nature of the pteropleuron and hypopleuron (*sensu* Comstock or Curran) is more obscure, and some sutures associated with them in other families are not evident in the Tabanidae. This is probably the reason why Bonhag (1949) refers to the hypopleuron simply as the meron. Crampton (1942) calls the hypopleuron the meropleurite to indicate a dual origin for the sclerite, and Snodgrass (1935) gives a similar interpretation. In many dipterous families a light-colored, horizontal streak much resembling membrane occurs near the dorsal edge of the hypopleuron; or, in some lower Diptera, an actual articulation occurs in that region separating the meron from the pleuron. The coxopleural membrane connects the two structures across the articulation.

In the Calyptratae except the Sarcophaginae and a few scattered groups, a vestige of the original coxopleural membrane persists as a "coxopleural streak." Above the streak the epimeron is divided by two sutures, a lower horizontal one completely separating the epimeron into a dorsal mesoanepimeron (the pteropleuron) and a ventral mesokatepimeron; and a second, upper suture, which is incomplete. The latter suture is called the subalar suture by Crampton (1942) and is probably of adventitious origin within the Diptera. Bonhag (1949) considered the subalar suture to be the mesoanepimeral suture, but a comparative study through several families of Diptera does not substantiate this conclusion. Actually, muscles analogous to those originating on the anepisternal suture and inserted on the basallare do not occur in connection with the subalare of *Sarcophaga bullata* Park. and possibly all Schizophora (they are absent in the horsefly also) so it may not be possible to establish the location of the anepimeral suture by means of muscle origins.

For systematic purposes it is convenient to retain the distinction between the katepimeron and the meron when fused, because they behave as independent sclerites as far as vestiture is concerned, even though no exact line of demarcation can be established. In a number of species hairs occur on the katepimeral region of the meropleurite, while the true meron is without setae; and, con-

versely, a number of species bear setae on the meral region, but have none on the katepimeron.

Meral, notopleural setae Setae occurring on the meron in calyptrates and, also, setae on the notopleuron, are peculiarly differentiated into two distinct types. The first, which may be called the primary setae, consists of the large macrochaetae, two of constant position on the notopleuron or a single vertical row on the posterior region of the meron. The row on the meron is roughly C-shaped with the setae near the ends of the row tending to become hair-like. The second type, the secondary hairs, occurs between, ahead and behind the macrochaetae of the middle part of the primary meral row; or, in the case of the notopleuron, scattered or sometimes localized in patches upon its surface. At the ends of the meral row, the secondaries would not always be distinguishable from the hair-like primary setae. In certain groups these two types vary independently and can be used as independent characters.

The presence or absence of secondary merals or notopleurals does not always give a good separation due to variation within single species of a few genera. This is not surprising as much the same pattern of variability is exhibited by no less than eight other thoracic characters consisting of the presence or absence of hairs on particular regions; e.g., upon the propleuron, prosternum, postalar wall, anatergite (infrasquamal setulae), metaepisternum, "metasternum," mesokatepimeron, and on the posterior surface of the hind coxa.

Besides the two primary notopleural setae in many Sarcophaginae two additional (rarely one), usually large setae occur, which are also of a constant position. These may be distinguished as subprimary setae of the notopleuron. They are characteristic of many Sarcophaginae, but they are often hair-like and virtually indistinguishable from secondary setae.

A few additional homologies are given by labels on Fig. 1. The basis for most of them will be found in Bonhag (1949).

Wing

Ventral setulae of the costa (Fig. 19) These are small, black setulae irregularly disposed on the ventral surface of the costa posterior to the antero-ventral row of "spines." In the Sarcophaginae ventral setulae are apparently always present on section II of the costa. In a few of these species the setulae are also found farther distad on section III (sometimes on the basal portion of section IV also). Their presence in this location is characteristic of *Sarcophaga bisetosa* Park. and North American relatives often placed in *Boettcheria*, besides a few unrelated species. In certain relatives of *Sarcophaga idonea* Ald. the setulae are usually present on section III, but occasionally are lacking; and in these species the usefulness of the character is limited.

Specialized setae, which may be distinguished as microtrichiae for the purposes of discussion, could be confused with the ventral setulae. The microtrichiae are never very numerous and are distributed at remarkably regular intervals along the dorsal and ventral surfaces of the costa. They differ, further, in being yellowish instead of black in almost all species, and in being curved to a greater extent than the setulae. The microtrichiae are not as large as the setulae. Both types of setae can be found intermixed on the ventral surface of costal section II if a very careful examination under high magnification is made.

Costal marginal setulae (Figures 20, 21) These are setulae occurring distal to the "spine" rows on the anterior margin of the costa—usually on sections V and VI. In some species the setulae do not exhibit free, projecting tips, but instead have become so closely appressed to each other and to the costa that they appear almost as a fused, transparent ridge.

A few instances have been discovered where the setulae are only partly appressed, and these occur in species related to *Sarcophaga aculeata* Ald. On the whole the character is not easy to use because of the frequency of specimens with battered wing tips. If the setulae are appressed, relatively rough treatment is required to obscure the condition; but, if the setulae are not appressed, they may be abraded off so that, without high magnification, the costa may seem to have a margin of appressed setulae. Microscope slides are desirable in a study of this character.

Microtrichiae The membrane of the primitive sarcophagid wing probably possessed a complete covering of microtrichiae; but many forms have arisen during the course of evolution which lack the covering to a greater or lesser extent. In general, the faster and more agile fliers possess more extensively bare areas than the slower species. The loss usually proceeds from the base of the wing outwards, and tends to occur ventrally and more frequently in the posterior region of the wing. It is interesting to note that most Sarcophagidae have the basal depression bare, but extremely few Tachinidae lack microtrichiae on this area. In other membrane regions the tachinids show the same tendency towards the loss of microtrichiae that the sarcophagids show.

The absence of microtrichiae on both dorsal and ventral surfaces is a readily recognized modification; since, by transmitted light, the area shows as a clear streak beside the microtrichiate surroundings. When the denuded areas are ventral only, they are best seen by shining a beam of light along the ventral side of the wing from base to tip. The microtrichiae are then apparent as shining points of light. It is most difficult to determine whether microtrichiae are absent ventrally from a dorsal view, unless the wing is on a slide.

For the purposes of description, it is convenient to subdivide cell

Cu₁. When examined from above, the membrane of this cell is seen to have two longitudinally directed furrows, the posterior one of which bends towards vein 1st A distally and occasionally forks near its extremity. These furrows may be referred to as the anterior and posterior Cu₁ cell furrows (Fig. 18).

Cell Cu₁ is thus roughly divided by the cell furrows into three regions: region 1, consisting of a narrow strip just posterior to vein M₃ + Cu₁; region 2, a wedge-shaped sector with the point directed basally between the two cell furrows; and region 3, shaped like a carving knife blade and situated between the posterior cell furrow and vein Cu₂ + 1st A.

Although the loss of microtrichiae from certain specific areas has occurred independently so many times that it cannot often be used to mark phylogenetic groups, there are a few instances in which some losses are indicative of relationship. *Saracophaga crassipalpis* (Macq.), *S. argyrostoma* (R.-D.) and *S. ruficornis* (Fab.) are justifiably linked on the basis of the loss of both dorsal and ventral microtrichiae on the anterior Cu₁ cell furrow, an association that can be supported by other characters. In a large group of species the same furrow, and other areas also, present microtrichiae which are very much smaller and sharply delimited from adjacent microtrichiae. This suggests stages through which an area may have passed before culmination in a now completely bare state. *Calypter hairs* These are fine hairs arising on the axillary cord and calypter membrane. They occur in two more or less distinct lengths, a short type, approximately twice the width of the axillary cord, and a longer type which is usually twice or more the length of the first. The longer hairs are usually restricted to the immediate vicinity of the angle between the upper and lower calypters. This condition is deviated from in the species groups associated with *Saracophaga cimbicis* Tns., *S. importuna* Walk., and *S. crassipalpis* Macq., in which the longer hairs are scattered among the shorter over nearly the whole length of the outer (lateral) calypter margin. The hairs often extend past the outer, hind corner and along the posterior margin of the calypter.

Legs

Apical tibial macrochaetae The dorsal, apical, tibial macrochaeta is a convenient reference point for locating others, and is that which would lie between the two regular, dorsal rows of setulae were they continued to the end of the tibia (dorsal, that is, when the legs are extended at right angles to the longitudinal body axis and in the horizontal plane).

The apical dorsal macrochaeta of tibia I is developed to a much greater extent than the apical anterodorsal in most sarcophagids, but at times the ratio is reversed, and the apical anterodorsal seta is the

larger of the two. Within the Sarcophagidae this reversed ration is useful in only a limited area, but in the Tachinidae this condition obtains in a large number of species in which it is so constant that no deviation from the ratio has been observed. In some species, as would be expected, the macrochaetae are approximately equal in size, but even then they are always nearly equal.

The presence or lack of well-developed apical posterodorsal or apical posteroventral macrochaetae on the hind tibia are similar characters which are helpful in classifying Sarcophagidae. Apical macrochaetae of the mid tibia do not seem particularly useful, but occasionally certain modifications occur, as the complete loss of the apical dorsal seta in one tachinid.

Spine row of hind trochanter A somewhat irregular row, rarely a single spine, occurs on the posterior surface of the hind trochanter of many species belonging to "*Blaesoxipha*," widest sense, and "*Boettcheria*." This row is present in both sexes and, in males, may occur alone or with a "brush."

Modified area of female mid femur This is a peculiar area on the posterior surface of the mid femur of the females of many *Sarcophaga*. It is difficult to characterize because it presents varying aspects. Perhaps the most constant mark of the area is a reduction in the pollinosity. When the area is most typical and well developed the pollen is practically absent, setulae are absent, and cross-hatched striations are present. The striations approach grooves in quality and are widely spaced. They may be apparently absent, or only one set of parallel grooves may be present. In dried specimens with dark femora the area is frequently reddish or orange.

Legend for plate on opposite page.

PLATE II. Structures of First Instar Larva

Fig. 2. Diagram of cephalopharyngeal skeleton based mainly on *Sarcophaga bullata* Park., lateral view.

Fig. 3. As Fig. 2, but dorsal view of anterior portions.

Fig. 4. *Erythrandra picipes* B. & B., dorsal view of cephalopharyngeal skeleton with vertical, lateral portions laid flat, labrum and mouth hooks omitted. (Approx. X230).

Fig. 5. *E. picipes* B. & B., labrum, lateral view at left, dorsal view at right. (Approx. X230).

Fig. 6. *Sarcophaga cooleyi* Park., labrum and epipharyngeal plate, dorsal view. (Approx. X230).

Fig. 7. *S. cessator* Ald., labrum and epipharyngeal plate, dorsal view. Approx. X230).

Fig. 8. *Sarcophaga varia* Walk., vestige of labrum and epipharyngeal plate, dorsal view. (Approx. X230).

Fig. 9. *Erythrandra picipes* B. & B., mouth hook, lateral view (Approx. X230).

Fig. 10. *Sarcophaga cooleyi* Park., mouth hook, lateral view, and anterior labial sclerite, dorsal view. (Approx. X125).

Fig. 11. *S. cessator* Ald., mouth hook, lateral view, and anterior labial sclerite, dorsal view. (Approx. X125).

Fig. 12. *S. varia* Walk., mouth hook, lateral view, and anterior labial sclerite, dorsal view. (Approx. X125).

Fig. 13. *S. querula* Walk., pseudotrachea, mesal portion at top, posterior at right. (Approx. X125).

Fig. 14. *S. cooleyi* Park., pseudotrachea, orientation as in Fig. 13. (Approx. X125).

Fig. 15. *S. varia* Walk., pseudotrachea, orientation as in Fig. 13. (Approx. X125).

Fig. 16. *S. sarracenioides* Ald., mouth hook, lateral view. (Approx. X125).

Fig. 17. *S. sarracenioides* Ald., dorsal view of appressed mouth hooks. (Approx. X125).

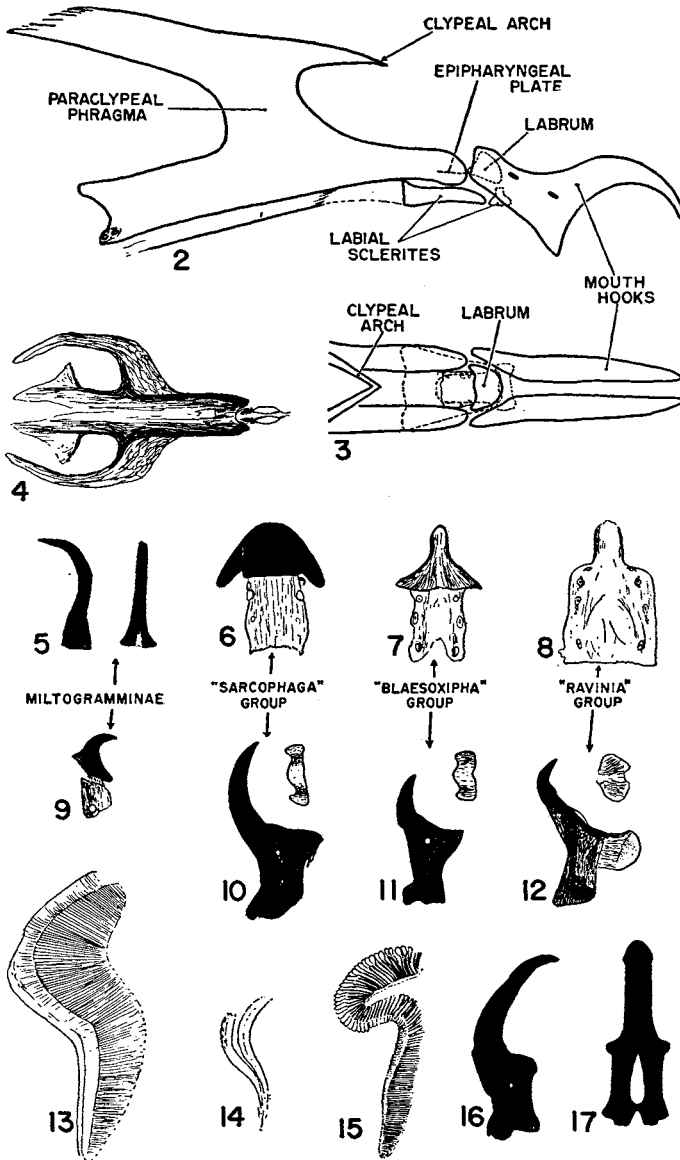


PLATE II

This area has been reported on by D'Assis-Fonseca (1953), who apparently thinks the area may be sensory, but, for the time being, it is better to use the less committal term, modified area. Freshly killed females with this area have been examined, and the area found to bear numerous small droplets of a clear fluid which evaporated in a few minutes leaving no visible trace. That this could be the result of condensation in the killing tube is possible, but a careful examination failed to reveal such droplets or even moisture anywhere else on the fly! It is interesting to note that the presence of this area in the females is highly correlated with the presence of villous hairs on the hind tibiae of the males of the various species; but there are some exceptions.

Preabdomen

Dorsum In the Sarcophagidae preabdominal tergites I and II are fused; and this syntergite has usually been referred to as the first "segment" by taxonomists, even when cognizant of the situation. The change required to accommodate the morphological facts may cause some temporary discomfort; but it is necessary if the numbering of the preabdominal tergites is not to be incongruous with that of both the preabdominal sternites and the postabdominal segments.

Subsequent tergites of the preabdomen show little modification except in some of the *Pachygraphia* (= *Camptops*) complex. In these, tergites I to V are fused into a one-piece shield along the mid dorsal region; but the fusion is not complete laterally, and some membrane occurs between the tergites. This modification is much commoner in the Tachinidae where it should prove more useful.

Erect hairs occur on the ventral aspects of tergites III to V (morphological) and serve as good characters for the females in particular of certain species. The males usually have erect hairs on all these regions, but there are a few which have the hairs decumbent. Examples of the different types of variation that may be found are as follows: *Sarcophaga cimbicis* Tns., no erect hairs on the

Legend for plate on opposite page.

PLATE III. Miscellaneous Structures of Taxonomic Importance

- Fig. 18. *Sarcophaga hunteri* Hough, wing. (Approx. X20).
 Fig. 19. *S. hunteri* Hough, enlarged view of costa adjacent to end of vein Sc, ventral view. (Approx. X55).
 Fig. 20. *S. hunteri* Hough, greatly enlarged view of wing tip (Approx. X250).
 Fig. 21. *Sarcophaga bisetosa* (Park.), greatly enlarged view of wing tip showing appressed marginal setulae. (Approx. X250).
 Fig. 22. *S. querula* Walk., ventral view of terminal sternite of female. (Approx. X30).
 Fig. 23. *S. impar* Ald., ventral view of terminal sternite of female. (Approx. X30).
 Fig. 24. *Opelousia obscura* Tns., lateral view of aedeagus. (Approx. X75).
 Fig. 25. *O. obscura* Tns., greatly enlarged view of anterior portion of sternite V of female showing alphaseta. (Approx. X100).
 Fig. 26. *O. obscura* Tns., Sternite V of female showing location of alphasetae. (Approx. X55).

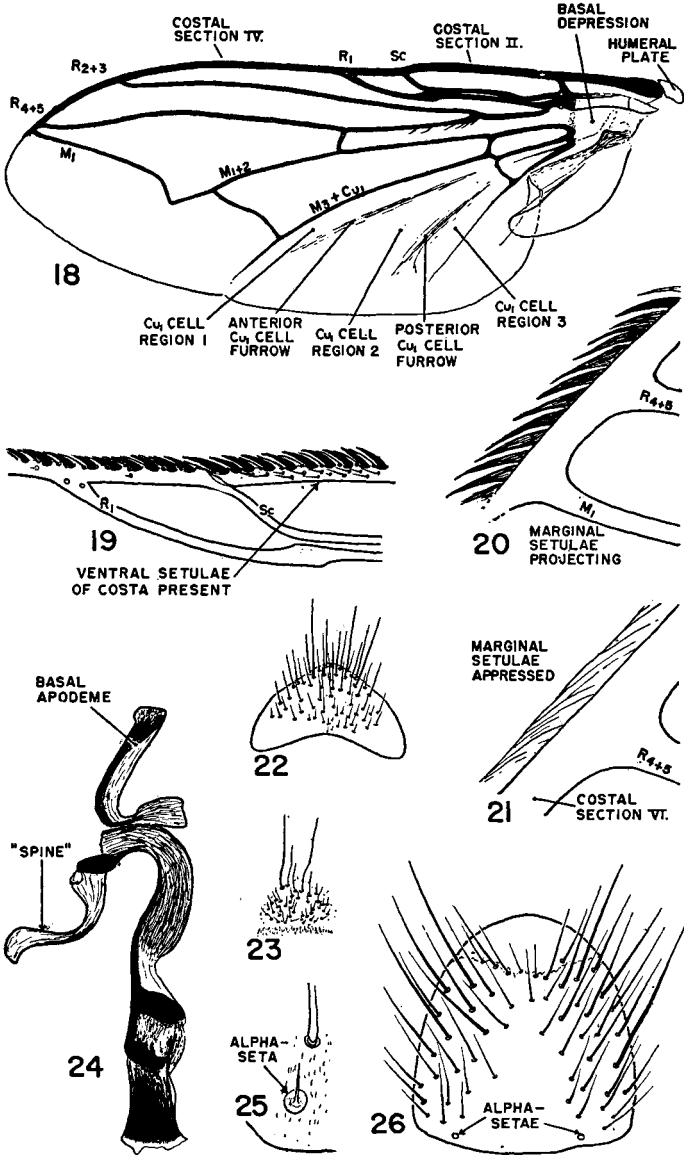


PLATE III

ventral aspects of these tergites; *S. querula* Walk., erect hairs on tergite V only; *S. ?laakei* Hall, erect hairs on ventral aspects of tergites IV and V; and *S. reversa*, erect hairs on the ventral aspect of all three tergites. These examples refer to the female only.

Venter—*alphetæ* (Figures 25, 26) In many calyptrates a pair of minute, transparent setae occurs at the anterior margin of each of the abdominal sternites II to V. These are scarcely visible under the highest magnification of a dissecting microscope, and usually the socket only is discernible as a small, round hole. The intersegmental membrane at the anterior edge of the sternite is normally carried ventrally and posteriorly by the preceding sternite so that the alphetæ are concealed in a sort of pocket. Sternites VI and VII of the female only appear to have structures homologous to alphetæ, but the exact nature of these structures has not been determined.

Alphetæ occur in Diptera besides the Calyptratae, but always appear markedly differentiated from other types of setae, being found only at the anterior margins of the sternites, or, in some lower Brachycera, at the anterior margins of some tergites in addition. Only one pair has been found per sternite in Schizophora, but in some Brachycera two pair occur.

1st Instar Larva—Cephalopharyngeal Skeleton

Clypeal arch (Figures 2, 3) The excellent paper by Snodgrass (1953) treats the major aspects of the first instar larva so adequately that little comment need be made. The so-called dorso-pharyngeal sclerite is inappropriately named, particularly since it is not a separate sclerite by the definition of the word. Since this "sclerite" is a part of clypeal portion of the fronto-clypeal plate, it may be termed the clypeal arch. The clypeal arch would then be defined as a transverse bridge of sclerotized material consisting of the anterior portion of the larval clypeus.

The clypeal arch may be considered to be incomplete in species in which the median portion of the arch is membranous. A few species, such as *Sarcophaga kellyi* Ald., represent an intermediate condition in which two, thin, lateral arms of the anterior clypeus curve medially and approach so closely that it is difficult to determine whether they are fused or not.

Labrum (Figures 2, 3, 5, 6, 7) The labrum of the first instar larva in most Calliphoridae, many Muscidae and the Miltogramminae, is as Snodgrass (1953) depicts it—a median lobe or hook just above the precibarial "atrium." This is termed the median hook or tooth by many systematists. A similar structure occupying a comparable position is of totally different origin in other groups, however. In the Rhinophorinae, according to Thompson (1934), the median hook is a composite consisting of the fused or closely associated mouth hooks. A similar but parallel development is found

in *Sarcophaga sarracenioides* Ald. and *S. aldrichi* Park. in which the mouth hooks are extremely closely appressed. A close relationship between these two species is suspect because of this condition.

Considerable variation occurs in the development of the labrum in the Sarcophaginae. In species of *Pachygraphia* the labrum is a very large, cushion-shaped object; in species of the "*Ravinia*" and "*Oxysarcodexia*" groups of *Sarcophaga* the other extreme occurs in which the labrum appears wholly membranous. The more typical *Sarcophaga* possess a labrum of intermediate development.

CLASSIFICATION

The present confusion of names and conflicting classifications for the nebulous groups within the Sarcophagidae are strongly reminiscent of the difficulties in the systematics of the Culicidae before F. W. Edwards introduced his admirable classification. Numerous small genera have not yet been ordered in any tenable phylogenetic system, although reasonable treatments, such as those of Aldrich (1916), Allen (1926), and Zumpt (1952), have been proposed, which do not purport to represent the complex phylogeny within the family.

It is now possible to make some improvements in these more general classifications by correlating some of the characters just described with others already in common use. Excluding a few difficult forms for reasons discussed later in this paper, it has been possible to segregate the species into the following categories, which are defined in the subsequent table. Many groups not specifically mentioned in the outline can definitely be placed in it on the basis of characters described in the literature, but there is always some doubt as to whether characters not mentioned will conform to the pattern.

Outline of Classification

MILTOGRAMMINAE:

AGRIINI—*Agria*, *Brachicoma*, *Erythrandra*, *Sarcophila*, *Wohlfahrtia*, and an unnamed genus.

MILTOGRAMMINI—all genera treated by Allen (1926), plus *Macronichia* and a few relatives.

SARCOPHAGINAE:

Includes many species—most of those treated by Aldrich (1916), many species described since, and a few forms such as *Neophyto setosa* Coq., but omitting Agriini as listed above.

Table of Major Phyletic Lines of the Sarcophagidae

1. GENERAL EXTERNAL CHARACTERS: coxopleural streak almost invariably present; posterior surface of hind coxa never with hairs; arista bare or pubescent in nearly all species; posterior surface of head rarely with whitish hairs; prosternum, postalar wall, and "metasternum" seldom with setae; never more than 2 notopleural macrochaetae.
MALE POSTABDOMEN: usually with 3 apparent postabdominal tergites, if 2, apparent first usually with suture or row of strong bristles anterior to marginal row indicating a fusion; anterior clasper completely

fused with "ninth sternite"; aedeagus consisting of one segment and often with basal, posterior "spine"; outer forceps usually elongate.

FIRST INSTAR LARVA: labrum well-developed as a large hook-like structure . . . MILTOGRAMMINAE.....2

GEN. EXT. CHARACTERS: coxopleural streak absent; posterior surface of hind coxa almost always with hairs; arista usually plumose; posterior surface of head usually with whitish hairs; prosternum, postalar wall, "metasternum" setulate in many species; subprimary notopleural setae present in the majority of species.

MALE POSTABDOMEN: with 2 apparent tergites; anterior clasper articulated with "ninth sternite," or, if fused, with suture-like line indicating junction; aedeagus commonly with a basal and a distal segment, sometimes one-segmented, rarely with basal, posterior "spine"; outer forceps seldom very elongate.

FIRST INSTAR LARVA: labrum not hook-like, relatively smaller, sometimes completely membranous.....SARCOPHAGINAE

2. First antennal segment projecting distinctly beyond edge of frontal lunule; infrasquamal setulae nearly always present; secondary meral hairs present Agriini

First antennal segment "flush" with frontal lunule, or else lunule completely concealed; infrasquamal setulae almost always absent; secondary meral hairs seldom presentMiltogrammini

This table is limited because of the incomplete sample of species upon which based. Nevertheless, there can be very little doubt that a primary dichotomy occurred in the evolution of the Sarcophagidae resulting in two major groups, the subfamilies; that a second dichotomy occurred in one of them yielding two subgroups, the two tribes; and, further, that these groups contain the majority of species classified in the family. However, there still remains the question of whether or not there are smaller groups, which should be accorded equivalent rank.

Until more information is obtained, three difficult complexes discussed later in this paper cannot be classified anywhere with certainty; and two of these accompanied a sample of species which are predominantly nearctic and neotropical. When the species of the world are considered, there will surely be more such species which should possibly be included in the Sarcophagidae as distinct subfamilies or tribes.

Rohdendorf (1937), in selecting the hairs on the posterior surface of the hind coxa as a primary character, made a fortunate choice as there are few exceptions to the general rule. Some species of the *Pachygraphia* complex and *Sarcophaga varia* Walk. (in contradiction to some indications in the literature) characteristically lack these hairs, and a few other species lack them occasionally; but, otherwise, these species are typical Sarcophaginae.

The presence or absence of the coxopleural streak is a more accurate character for placing the species of this study because there is only one observed exception. *Opsidia gonioides* Coq. lacks the streak, but is obviously a typical Miltogrammini. This type of deviation might be expected on the basis of the independent losses of the streak in other families of the Calyptratae, which indicate that the

streak is not indispensable to the fly. *Orthellia caesarion* (Mg.) is one of the few Muscidae without the streak, and many Calliphoridae do not exhibit it. On the other hand, to find a species of Sarcophaginae with the coxopleural streak would be surprising, since its absence in so many diverse groups of the subfamily suggests that the ancestor of all of them lacked it.

The following statements may be made about two other characters varying in a manner similar to that of the coxopleural streak: la. The complete fusion of the anterior clasper to the "ninth sternite" in the male in both the Agriini and the Miltogrammini suggests that the ancestor of both possessed the same condition.

lb. Within the Sarcophaginae species having a tendency towards fusion of the anterior clasper with the "ninth sternite" suggest the possibility of complete fusion having occurred in other species, which would then be inseparable from Miltogramminae on this basis.

2a. The occurrence of but two apparent postabdominal tergites in the males of the diverse groups of the Sarcophaginae suggests that the common ancestor of all had but two.

2b. The tendency towards reduction of the first apparent tergite of the postabdomen of males of certain Miltogrammini, or the greater or lesser degree of fusion in the Agriini indicates the possibility of a condition paralleling that in the Sarcophaginae. From the literature description, one apparent Agriini, *Xiphidiella* Zumpt (1952) is like the Sarcophaginae in this character. *Eumacronychia sternalis* Allen has but two apparent tergites in the male postabdomen, the first being reduced to membrane.

Nearly all Miltogramminae have a pubescent or bare arista, but among the Sarcophaginae there are several exceptions to the plumose arista. *Neophyto setosa* Coq. has a micropubescent arista, and a whole series of South American species of Sarcophaginae have a bare or sometimes long pubescent arista.

Other characters which are qualified in the table deviate only sporadically within the groups they are characteristic of, and there is little correlation among the exceptions. We may reasonably assume that these exceptions are merely of independent origin within their groups and have no special phylogenetic significance as far as the major phyletic lines are concerned.

Certain groups of genera, which have been classified near the Sarcophagidae in the past, are possibly incorrectly associated with them. These forms, the Rhinophorinae, *Opelousia* and allies, and *Mimodexia* deserve considerably more study as there is some evidence that these are not closely related to the Sarcophagidae.

Séguy (1941) regards the Rhinophorinae as one of the subfamilies of the Calliphoridae, to which family he also assigns the Sarcophagidae of this paper. Townsend (1935) treats the group as

the family Melanophoridae, which he includes with the Sarcophagidae and Calliphoridae in the "Muscoidea." The Tachinidae belong in a separate superfamily, the "Oestroidea," according to him. These placements of the Rhinophorinae seem to have been made mostly on the basis of the undeveloped infrascutellum.

Thompson (1934) suggests the possession of two distinct mouth hooks by the first instar larva of a species of the Rhinophorinae indicates an affinity with *Sarcophaga*. Three things may be said about this, however. First, if the prototype first instar of the calyptrates is a larva with two distinct mouth hooks (with a relatively undeveloped labrum), the primitive ancestors of the Tachinidae may also be expected to exhibit this condition; which, consequently, could be retained in less specialized extant forms. Second, the first instar cephalopharyngeal skeleton of a tachinid was recovered by dissection of a larva of *Dendroides cyanipennis* Lat. (Coleo.: Pyrochroidae) from which the third instar larva and the exuviae of the second instar had been removed. In this species the mouth hooks are very closely associated so as to appear as a single median hook, and dissection is necessary to demonstrate the double nature. Third, even the assumption that the primitive ancestral stock of the calliphorid-sarcophagid stem possessed a recessive labrum with well-developed mouth hooks is open to question, since many Muscidae, Calliphoridae and the Miltogramminae all have a large hook-like labrum with relatively smaller mouth hooks.

On account of this, it would be quite in order to hypothesize that the Sarcophaginae underwent specialization by a reduction of the labrum and a greater development of the mouth hooks. Townsend (1935) claims that *Neophyto* sp. has a well developed labrum, which, if correct, would lend very strong support to this hypothesis, and establish *Neophyto* as a primitive Sarcophaginae. (Other characters in this species are also relatively primitive.) Thus, a consideration of the data relating to the first instar labrum and mouth hooks does not necessarily link the Rhinophorinae to *Sarcophaga* and the Sarcophaginae.

Of the Rhinophorinae, only *Melanophora roralis* (Linn.) was seen, but in this single species there is evidence of a closer relationship to the Tachinidae than to the Sarcophagidae. Contrary to some statements in the literature, all of the preabdominal sternites of this species are overlapped by the tergites, and there is a small, but nevertheless distinct infrascutellum developed. Thompson (1934) reports that a close relative of *M. roralis* deposits eggs which require a fairly long period for the development and hatching of the larva. This is more in harmony with the known biology of some Tachinidae than it is with that of the Sarcophagidae.

The spiracles of the female postabdomen of *Melanophora roralis*

(Linn.) are both associated with their respective tergites and seemingly represent among calyptrates a primitive state in which the seventh abdominal spiracle has not migrated forward into tergite VI, as is the case in all known Sarcophagidae. This information could well mean that *M. roralis*, at least, is an early specialized, but essentially primitive derivative from tachinid stock; but the other sow-bug parasites need further study.

The exact relationships of *Opelousia* and allies are not clear, but the species are only poorly known. None of the established morphological peculiarities of any one of the calyptrate families occurs in this group, so they often end up as a residue from keys with the Sarcophagidae. The possession of alphasetae by these species may connect them with the calliphorid stem; since these setae have been found in all of the few Calliphoridae dissected for this study, but in none of the Sarcophagidae. The female terminalia of *Opelousia* and most Calliphoridae are strikingly similar, and both are on the order of a telescoping tube. From the structure of the uterus it is more probable that *O. obscura* Tns. lays eggs rather than larvae. It is possible, though, that the ancestral Sarcophagidae exhibited these characters.

Mimodexia, judging from Rohdendorf's (1937) description and figures, is most unusual for a sarcophagid. The figures of the aedeagus so much resemble those of some Calliphoridae that it would seem wise to investigate this genus further before definitely regarding it as a sarcophagid.

The classification proposed here resembles Rohdendorf's more closely than any other. Probably some of his subfamilies should be united within the groups defined earlier, but it is best to defer such treatment until the species in question can be more thoroughly examined. The Agriini including *Wohlfahrtia*, however, do not seem best treated as a separate subfamily, because the evidence overwhelmingly indicates a very close affinity with the tribe Miltogrammini. Biological differences are sometimes given undue weight, but they are not as clear-cut as may be thought; nor, in fact, is the biology for many of the species even known. Species of *Brachicoma* have been reported more than once to be associated with Hymenoptera as the Miltogrammini are; and it is easy to demonstrate a multitude of morphological similarities linking *Brachicoma* with *Wohlfahrtia* and other Agriini. Recently it has been shown that a typical Miltogrammini, *Hilarella hilarella* (Zett.) is parasitic on a species of Orthoptera (Arnaud, 1953).

The more detailed classifications, based mainly on species not found in the New World, cannot be evaluated properly on the basis of a study of the New World fauna, except in their broader aspects. Hence, further remarks concerning Rohdendorf's or sev-

eral of the other classifications are not entirely appropriate for this paper.

Other classifications do include New World forms, and deserve comment. Apart from the more conservative treatments mentioned earlier, these classifications represent a great deal of untruth. The authors have, in fact, failed to understand a basic tenet of systematic methodology, since they have implicitly assumed that their limited set of characters was adequate to construct a natural classification. With the principle of priority in effect, any claims of tentativeness in such cases are actually without meaning if the authors "define" and give new names to all sizes of categories from subgenus to family. The various alterations of the current group concepts necessitated by the characters presented in this paper make it clear that our knowledge regarding the Sarcophagidae is much too rudimentary to permit construction of a detailed phylogeny. Within the Tachinidae there are similarly other apparently new characters that indicate that considerable regrouping will be necessary.

The same methodological error is prevalent in a milder form among certain contemporary systematists in the idea that the male terminalia offer the soundest basis for grouping species, and that they should be the prime object in a study of phylogeny. The evidence does not indicate that the adult calyptrate is deficient in external characters of phylogenetic significance, nor does it support the assumption that any *single* character of the male postabdomen is more reliable than any other single character. A fairly high degree of reliability may be expected from conclusions drawn from a thorough study of the male postabdomen, but this reliability is the result of correlations among more than one character.

Townsend (1934-1942) presents one of the most complete classifications of the Calyptratae ever proposed. Many characters are used, but many are superficial and have resulted in a correspondingly superficial classification. Very often placements have obviously been made on the basis of general habitus or on relatively insignificant variations in the morphology of the head. As a result the keys in this work are nearly impossible to use.

Townsend's (1938) *Miltogrammini*, *Macronichiini*, and *Metopiini* belong with few exceptions to the tribe *Miltogrammini*. The divisions within this group cannot be established yet, but it is certain that Townsend's tribes do not form natural subdivisions of the *Miltogrammini*. *Phrosinella*, for instance, is found in his *Miltogrammini* despite many characters, such as the very unusual occurrence (for the Sarcophagidae) of setulae on the frontal lunule, relating this genus to *Metopia* of his *Metopiini*. Yet, also included in the *Miltogrammini* are *Senotainia* and *Amobia*, which can be associated with *Macronichia* on the basis of the knob-like develop-

ment of the lower propleuron bearing three differentiated macrochaetae, besides other characters.

Townsend's Agriini contains mostly non-agriine genera, and one finds true Agriini scattered elsewhere. *Erythrandra* B. & B. is an example misplaced in the Myorhinini.

More glaring misplacements are to be found in the Morinini of an entirely separate "family," the Melanophoridae. Here one finds *Camptops*, synonymized by Aldrich with *Pachygraphia*, which is clearly a Sarcophaginae. This genus may be linked with *Stenopyga* and some allies of Townsend's Stephanostomatini on the basis of the fusion of all of the preabdominal tergites along the mid dorsal region, a character which apparently does not occur in any other Sarcophagidae. Both male and female terminalia are in conformity with this grouping.

Brauer and Bergenstamm's classification (1889, 1891) is somewhat understandably inaccurate because of the time in which produced. It exhibits much the same type of misplacement that Townsend's does, and the authors similarly show a marked predilection for head characters and "splinter genera." There appears to be little need for comment on their system, since it has not been widely accepted.

Roback (1954) proposes the most recent and complete phylogenetic classification of the Sarcophaginae, which is based primarily on modifications of the aedeagus. In the light of many characters drawn from sources other than the aedeagus, numerous points of his classification must be rejected. The incorrect association of the Agriini with Sarcophaginae has already been discussed.

Sarcophaga impar Ald. has been removed to a separate subtribe of the Sarcophagini and placed in a new genus, *Imparia* Roback, which constitutes "the most primitive of the subtribes" of its tribe. But, *Sarcophaga kellyi* Ald. is found in the Boettcheriina. If the male postabdomen and fifth sternite or the female terminalia are not used, these two species are almost inseparable in the adult stage. The characters listed below suggest that these species are not only related, but are closely related.

1. Posterior surface of hind trochanter with a short, irregular row of stubby bristles, much resembling the spines of the "brush," but situated on a different area and occurring in both sexes.
2. Posterior surface of mid femur of female with a modified area lacking setae and with reduced pollen, of approximately the same size and in the same position near the middle of the femur in both species.
3. Abdominal sternites VI to VIII of female fused, and sternite VIII darker, thicker, and much smaller than the preceding two.
4. Larva of both species easily reared on decaying beef.
5. Labrum of first instar larva relatively reduced, thinly pigmented,

and pigment separated into two lateral areas by a longitudinal, relatively clear stripe.

6. Third instar larva of both species, at least externally, identical for all practical purposes, yet remarkably distinct from other species including those placed in the same subtribe as *Sarcophaga kellyi* Ald., such as *S. cimbicis* Tns., *S. latisterna* (Park.), and *S. importuna* Walk.

Sarcophaga plinthopyga v.d.W., for which another new and certainly superfluous subtribe is proposed, may be collected in a small group of closely related species, including *S. kellyi* Ald., *S. impar* Ald., and *S. cessator* Ald., on the basis of many characters. This group, and consequently, Roback's Impariina and Hystriocnemina may be united with most of his Servaisiina, some of his Boettcheriina, and a few of his Sarcophagina to constitute a "*Blaesoxipha* group," corresponding to a somewhat extended version of *Blaesoxipha* of several European authors. These may be opposed to a "*Boettcheria-Metoposarcophaga* group" (with which Roback associates some *Blaesoxipha* group species) on the basis of the following characters:

Blaesoxipha group:

1. Postalar wall setulate, except occasional females of *Sarcophaga hunteri* Hough.
2. Ventral metaepisternum never with setae.
3. Long hairs of lower calypter restricted to immediate vicinity of angle between upper and lower calypter, not extending farther than half distance from angle to outer, hind corner of calypter.
4. Ctenidium present on posteroventral edge of male mid femur.
5. Apical portion of inner forceps with a patch of peculiar, minute spines on postero-lateral surface.
6. Sternites VII and VIII of female postabdomen fused.
7. Spiracle VI of female postabdomen located in tergite VI, with few exceptions *within* individual species.
8. Labrum of first instar larva apparently never well-developed, only faintly pigmented.
9. Clypeal arch of first instar larva usually incomplete; complete or nearly complete in a few of the apparently more primitive species of the group, such as *Sarcophaga plinthopyga* V. d. W., *S. impar* Ald., *S. kellyi*, and others.

Boettcheria-Metoposarcophaga group:

1. Postalar wall without setulae.
2. Ventral metaepisternum above hind coxa with fine hairs in most species.
3. Longer hairs of lower calypter extending along outer (lateral) margin nearly to or beyond outer, hind corner of calypter.
4. Mid femur of male without ctenidium.

5. Apical portion of inner forceps of male without spines, only minute hairs present.

6. Sternites VII and VIII of female postabdomen articulated, rarely closely associated.

7. Spiracle VI of female postabdomen in the membrane ahead of the tergite.

8. Labrum of first instar larva well-developed and heavily pigmented.

9. Clypeal arch of first instar larva complete.

The subdivisions of the *Blaesoxipha* group are not clear, and there are many new species included. The *impar* group, including *kellyi*, *plinthopyga*, and others may be comparatively primitive, since they are easily reared on meat and possess a complete clypeal arch. Other *Blaesoxipha* group species appear to be obligate parasites. Perhaps the most aberrant member, if it be a true member, is *Sarcophaga salva* Ald., which deviates from the usual set of characters in several details.

Roback's "*Acandotheca*" (*Lepyria*) *melampyga* (Ald.) of his *Servaisiina* cannot be associated with the *Blaesoxipha* group at all. The male has nearly straight inner forceps, which lack the characteristic patch of small spines, and does not have a mid femoral ctenidium. The possession of a patch of whitish hairs on the sides of the scutellum, the anterior displacement of the marginal macrochaetae of tergite V (morphological) of the female postabdomen, the setulate R₁, and the usual possession of two approximated macrochaetae on the posterior surface of the fore tibia suggest a relationship with species; such as, *Sarcophaga ampulla* Ald. Further, *Acanthodotheca* is misspelled "*Acandotheca*," and the new subgenus, *Lepyria* Roback, is undoubtedly synonymous with *Titanogrypa* Townsend, which was apparently overlooked.

It is possible to take issue with Roback on several more points of phylogeny, but the above examples suffice to show the result of faulty methodology. Objections of a somewhat different nature may be made to the postulated characters of the archetype of the Sarcophaginae and to nomenclatorial treatment.

A bare arista is postulated for the archetype; but, since a plumose arista is found in both the Sarcophaginae and Miltogramminae, it is just as logical to consider the bare aristas of the various groups as independent specializations. The occurrence of a plumose arista in primitive members of related calyptrates; such as, the *Opelousia* group and some Calliphoridae, may be adduced as more conclusive support for this idea.

Another postulate proposes for the archetype an aedeagus consisting of two segments, the "phallophore" and the "phallus." After consideration of the pertinent evidence, however, one is almost compelled to pose the contrary, but more logical postulate, that

the aedeagus of the archetype consisted of but one segment. In both the Calliphoridae and the Miltogramminae (with a few apparently derived exceptions, where the aedeagus is also one-segmented) a similar type of aedeagus is found, which consists of a single segment. Essentially, the segment is a membranous tube supported by a longitudinal, rod-like sclerotization of the posterior wall from which variable extensions and projections originate, and it is the common type of aedeagus occurring in the calyptrates with primary meral setae. This leads to the proposal that the aedeagus of the Sarcophagidae was one-segmented, at least until the time when the Sarcophaginae diverged from the Miltogramminae.

With this in mind, one may well suspect that the aedeagus of the "Raviniina" of Roback is not secondarily derived, but is primarily one-segmented. This seems reasonable, since many of the "Raviniina" exhibit the most primitive food habits known for the family Sarcophagidae.

There is so little evidence bearing on the problem of the origin of the Calliphoridae-Sarcophagidae stem that it is almost a waste of time to speculate on the matter without obtaining more data. There seems to be very little to relate the Sarcophagidae to the Scopeumatinae of Roback, and the articulation in the aedeagus of the latter is undoubtedly of independent origin from that in the Sarcophaginae. A similar articulation does occur in some Tachinidae also.

The term "phallus" in recent morphological parlance usually denotes the aedeagus plus other parts; and the application of this term to a portion of the aedeagus by Roback is somewhat disturbing. It would probably have been better to apply arbitrary terms to the various parts of the complex until the homologies with lower Diptera are worked out. Roback appears to have accepted much of this terminology from Crampton (1942) from whom he also may have obtained the idea that the aedeagus of *Phormia regina* (Mg.) is two-segmented—an idea that would support his postulated primitively two-segmented aedeagus. *Phormia regina* (Mg.) does *not* have a two-segmented aedeagus; the posterior sclerotized rod is continuous just as it is in most other (or all?) Calliphoridae.

In regard to nomenclatorial treatment, Roback establishes three subtribes for the Agriini after examining a single species of each of the three type genera, plus literature figures for additional species of these genera. In view of the fact that there are many genera of Agriini, including some in North America, which were not seen; it does not seem possible that the relationships within the Agriini could be determined from such a small sample. Furthermore, several different names of the "family-group" category have been proposed for Agriini, which Roback does not mention. These names would have priority over both Wohlfahrtiina and

Sarcophagidae in the case that the type genera are appropriately grouped.

Also, *Sarcophagula* and *Sarothromyia* are synonymized (which even the most conservative authors have treated as distinct). For the included species Roback erects a new subtribe, the Sarcophagulina, but does not mention the Sarothromyinae, established by Hall (1932).

Some excellent points of Roback's work are to be found in his association of the "*Oxysarcodexia*" and "*Ravinia*" species, and, of course, in his elucidation of the parts of the apical segment of the aedeagus. Some of these structures, as Roback mentions, may be of polyphyletic origin, but such cases should be detectable if other characters are considered. The *Oxysarcodexia-Ravinia* grouping is supported by other morphology; such as, the membranous labrum and greatly developed pseudotracheae of the first instar larva (Fig. 13, 15) and the sclerotized terminal sternite of the female postabdomen (Fig. 22), which is distinct from the membranous terminal sternite characteristic of other Sarcophaginae (Fig. 23).

Attention may be called to two more problems resulting mostly from differences of opinion among systematists dealing with sarcophagids. Many authors regard the Sarcophagidae of this paper as a subfamily of the Calliphoridae, and they have much evidence in their favor. Not one of the many characters currently used for distinguishing the two groups is without exception, and genera such as *Opelousia* might constitute true connecting links. At any rate, the decision to treat the Sarcophagidae as a separate family is no better supported than one placing them as a subfamily of the Calliphoridae. When a more intensive study of the systematics of these groups is made for the world, it should be possible to determine whether it is more practical to treat them as distinct families, or as a single family.

The only character with no apparent exception at the moment is the presence of the alphasetae in the Calliphoridae, but this has been checked through so few species that it is not established for this family. Within the Sarcophagidae there appears to be no exception to the non-protrusion of the prothoracic spiracular horns of the pupa through the puparial wall, but at least one calliphorid is similar in this respect. In the larva the posterior cavity of *Sarcophaga salva* Ald. is no deeper than that of some Calliphoridae; and, although *Sarcophaga sinuata* Mg. has a deep cavity in the third instar, this cavity is nearly obliterated when the puparium forms.

True intrapostocular cilia do not occur in the Sarcophagidae, but some males of *Sarcophaga utilis* Ald. have small setulae ahead of the first row of postocular cilia, which would certainly be mistaken for intrapostocular cilia by a person not familiar with the character. There are so many exceptions to characters of the chae-

totaxy of the notopleuron, prosternum, propleuron, or degree of plumosity of the arista that these are little more than "rule of thumb" guides when the species of any large area are treated.

The other difference of opinion centers around generic concepts within the Sarcophaginae. Attempts to subdivide *Sarcophaga*, *sens. lat.*, are probably premature, because the complicated relationships within this genus are basically unknown. A person may be able to establish the affinities of many of the species of his own faunal region; however, many new aspects to such a limited system are brought to light when species from other regions are considered, and it is most doubtful that the available literature contains sufficient information to allow a person to do this vicariously. It is surely more appropriate for systematists to solve the phylogeny first and then to name the groups, rather than to name first and be confronted with the headaches of involved synonymies afterwards.

Problems entailed by untimely splitting can be illustrated by some of the possible treatments of the species of the *Blaesoxipha* group, as delimited earlier. No trouble is experienced in recognizing all of them as members of *Sarcophaga*, *sens. lat.* If the *Blaesoxipha* group is elevated to genus, the difficulty of classifying *Sarcophaga salva* Ald. and, perhaps, the pitcher plant species becomes a problem. If *Blaesoxipha* is further divided, a greater number of similar difficulties is encountered, and, on top of this, one begins to wonder which, if any, of our American species should be treated as *Blaesoxipha*, or *Tephromyia*, or *Locustivora*, etc., etc.

Some authors have favored disintegrating *Sarcophaga* to the extent that every morphological variant is isolated in its own genus. This may avoid long synonymies, but it also undermines a prime function of the systematist, which is to present to the non-specialist a practical system of classification. It is generally conceded that generic limits are a subjective matter, but principles of convenience and practicality cannot be ignored in forming a generic classification. Although a specialist can readily recognize the most restricted genus, an inexperienced person may have considerable difficulty, yet it is not so difficult for the non-specialist to identify to genus when generic limits are broader.

Very cogent arguments for retaining *Sarcophaga*, *sens. lat.*, or its larger subgroups at the generic level can be drawn from the analogous situation in the Culicidae. In spite of the inclusion of "different" species, the utility of such concepts as *Aedes*, *Culex*, or *Anopheles* is manifest. If these mosquitos were scattered among the many small genera as they once were, there is no doubt that they would not be so easily comprehensible as they now are.

The objection that the Sarcophagidae are a rapidly evolving family with ill-defined group limits is without basis. The relative

ease with which it was possible to clarify the major divisions within the Sarcophagidae offers ample proof that the confusion resulted not from some intrinsic property of the species, but from a deficiency of pertinent data. There is absolutely no reason to doubt that a similar situation obtains for lower levels. The characters which may be cited in support of the *Blaesoxipha* or *Ravinia* groups are already suggestive of possible solutions when sufficient information is accumulated.

When it is advantageous to recognize divisions within larger genera, the application of subgenera is warranted. This treatment does not diminish the utility of the large genus, and at the same time facilitates discussion of smaller groups. As has been stated before, however, the relationships within the Sarcophaginae are so obscure that it is probably best to wait until these relationships are understood instead of compounding the present nomenclature with more supraspecific names. The amount of inconvenience caused by the necessity of talking about groups of species instead of "genera" is small compared to the inconvenience caused by the numerous conflicting generic classifications.

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