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SOME COMMENTS ON THE TRIBAL CLASSIFICATION OF ASILIDAE (DIPTERA)

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A B S T R A C T

Critical comment on the classification of Asilidae with special reference to F. M. Hull's work "Robber Flies 6f the World" (1962) is given. Suggestions are made for merging rather than proliferation of genera and tribes.

The year of writing, 1972, is just ten years since the publication of F.M. Hull's two-volume work [1] *Robber Flies of the World', so* when I was honoured with an invitation to contribute an article in commemoration of Professor Theodor's seventy-fifth birthday I thought that this might be an appropriate occasion on which to make a few observations arising out of this book.

Professor Theodor has made major contributions to the taxonomy and biology of Phlebotomidae, Nycteribiidae, and Hippboscidae, as well as illuminating studies of particular aspec, -; of other families that are conspicuous in the dipterous fauna of Israel, notably Tabanidae, Bombyliidae and Asilidae.

Professor Hull's book was a landmark in the taxonomy of Asilidae, Until then no author had attempted to survey the family as a whole, even on a regional basis, and certainly not in anything like this comprehensive way. The last 300 pages alone might well have been published separately as a unique "Atlas of Asilidae". They form an invaluable reference book, giving drawings of antennae, the head from two angles, male and female genitalia for one species at least of every described genus. There is also an almost complete bibliography of all papers since Linnaeus that include descriptions of Asilidae.

This part of the book is objective. No comments are passed, nor any opinions expressed, and since the species illustrated is usually the type-species of the genus, the figures have an authenticity that is rarely achieved by taxonomic works. The rest of the book, the first 600 pages, is quite different. It is equally comprehensive, but consists almost entirely of descriptions, expressions of opinion, and comment on the published opinions of others. After preliminary discussions of morphology, biology and geographical distribution, we proceed by means of keys to subfamilies, tribes and genera. Each genus is described at length, and each is provided with a list of included species, arranged geographically.

On this scale it was obviously quite impractical for the author to examine each species critically, and thus provide a world revision down to species-level. In fact no specific judgments are offered, and the only new species described are the types of new genera. The others are lists of names, conscientiously compiled from the literature, and usefully indexed, so that any elusive species in this large family can now be rapidly located in at least a provisional genus.

Some of the preparatory work for this book was carried out at the British Museum (Natural History) in London, and I think it is fair to say that the accounts of genera were based almost exclusively on study of the type-species. Hull is acutely interested in the probable evolution of Asilidae, and frequently makes observations like the one on p. 47: "It is possible that through *Codula* Macquart on the one hand, and *Chryseutria* Hardy on the other we see a group which has a surviving member in three different stages of the past history of the group?". Yet very rarely does he discuss variation within a genus, and this is the greatest shortcoming of Hull's book.

On the other hand Hull freely discusses his classification of genera into tribes and subfamilies, and these sections provide a convenient starting-point for the present essay.

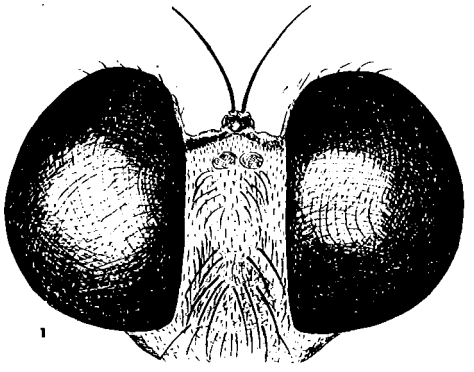
Asilidae are one of the biggest families of Diptera, and also one of the most clearly defined. All known members are actively predacious on other insects or on spiders, and

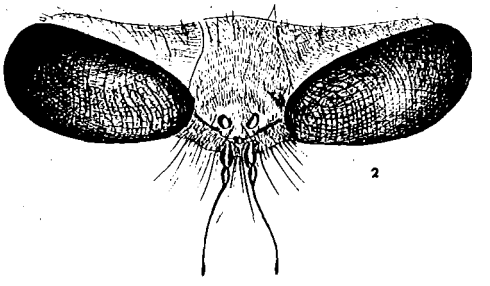
their external structure is adapted to this purpose in many obvious ways. The feature that is most often mentioned as diagnostic of Asilidae is that the vertex of the head is 'sunken between the eyes' (Fig. 1), though this is not invariably so. This characteristic can be interpreted in the opposite sense, that the eyes project above the level of the vertex, and can be seen as part of the perfection of the eyes into a capable binocular organ for observing prey. Some Asilidae have strongly rounded eyes (Fig. 3), but in some---notably Xenomyzini (Fig. 2)--- the eyes are noticeably flattened, and directed mainly forwards. Most asilids have larger facets facing forwards, near the level of the antennae.

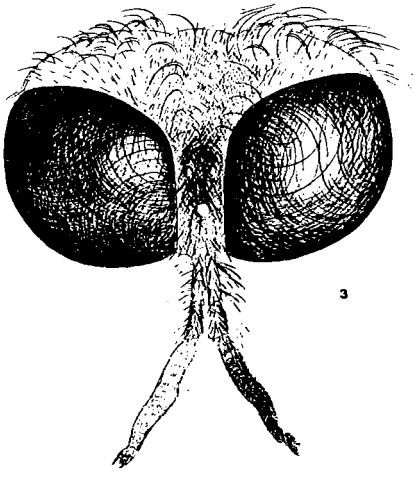
Almost diagnostic of Asilidae is the mystax, or moustache (M), an assembly of downturned bristles between the eyes and above the mouthmargin. Looking at the proboscis projecting forwards and downwards, and remembering that prey is impaled alive on this and sucked dry, the mystax as well as the softer hairs of the 'beard' seem obviously protective in function, keeping the struggling prey away from the eyes of the robber fly (Fig. 4).

The legs of Asilidae are obviously built for standing, and for grasping prey. If they are compared with those of *Bombylius*, delicate legs used for steering in flight (Nachtigall, 1974), and to balance on a flower while feeding, the legs of even fragile Asilidae such as *Stichopogon* are seen as spiny prehensile organs. Sometimes, as in *Gonioscelis* (Fig. 5), the forelegs have become formidable weapons.

It is evident therefore that the most characteristic structural features of Asilidae appear to be directly functional, i.e. adaptive. Classification of such a family can be no academic exercise, with facile segregation of 'plesiomorphic' and 'apomorphic' characters, whatever these may mean. Any classification of Asilidae is largely intuitive, with judgments based upon a consensus of structural and biological characteristics. Few structural characters can be said with certainty to be non-adaptive. Even wing venation, though not obviously so, must be adaptive in the sense that closure of cells by the meeting of veins must make particular areas of the wing more rigid, and thus alter its characteristics in flight.







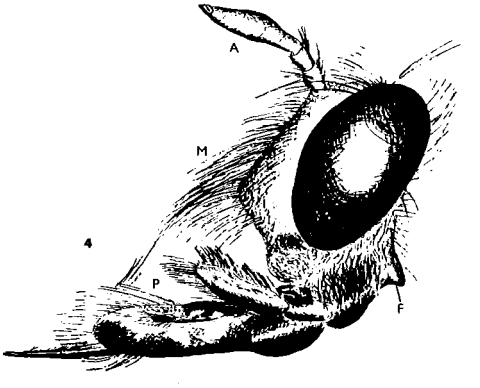


Fig. 1. Head of *Maira* (Laphriini) from in front, showing the 'sunken vertex' characteristic of most Asilidae, though often less pronounced than this.

Figs. 2,3. Heads of two Asilidae in dorsal view, to illustrate extremes of shape: 2, *Xenomyza* (Xenomyzini) with 'goggle eyes' which direct most of the facets towards the front; 3, *Gonioscelis* (Saropogonini), with almost spherical head, giving a good all-round view.

Fig. 4. Head of *Stiphrolamyra* (Laphriini), showing the heavy protective bristles of mystax (M), palpi and proboscis (P); the posterior flange common to most of Hull's tribe Ctenotini (F); and the antennal flagellum (A), showing traces of segmentation.

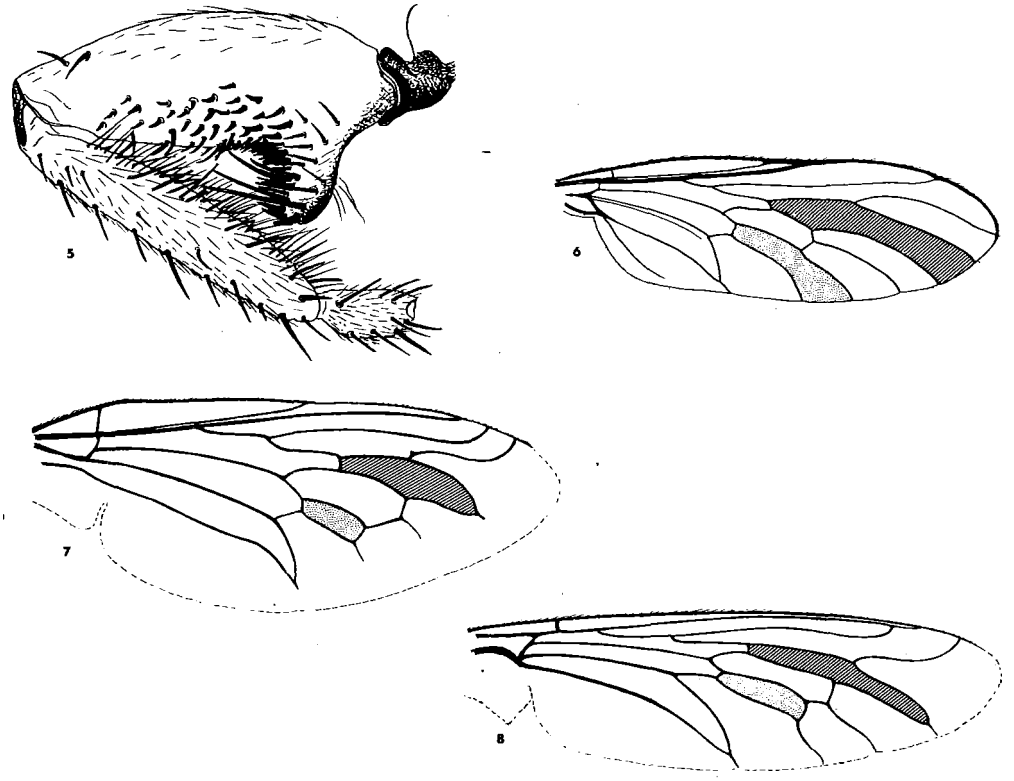


Fig. 5. Femur, tibia and basitarsus of the fore-leg of *Gonioscelis* (Saropogonini), showing development of spines characteristic of this genus, and apparently prehensile in function.

Fig. 6. Wing of *Oligopogon* (? Xenomyzini), showing all the cells along the wing margin open, except the anal cell. 4th posterior cell stippled; 1st posterior cell cross-hatched.

Fig. 7. Wing of *Sisyrnodytes* (Saropogonini), a specialised wing in which the unsupported and flexible hind margin is braced by the closure of the first (cross-hatched) and fourth (stippled) posterior cells, as well as the anal.

Fig. 8. Wing of *Nusa* (Laphriini), with some specialisations similar to those of *Sisyrnodytes* (Fig. 7). First posterior cell cross-hatched; fourth posterior cell stippled.

An example of an intuitive judgment is the conviction that a series of open cells around the wing margin (except usually for the anal cell) is plesiomorphic, and the closure of these is apomorphic. The fourth posterior cell is the first to be affected, and it is perhaps significant that this is the next cell forwards that can easily be closed (Fig. 6) : I am not aware that the fifth posterior cell is ever closed, even in families such as Mydaidae and Syrphidae, with a proliferation of closed cells. A glance at the drawings of wings in Hull's book, especially from about Figs. 440-606, will show how the variations are played on these two cells, while the closure of the first posterior cell appears as an arbitrary specialisation, except in wings like *Sisyrnodytes* and *Nusa* (Figs. 7,8), where the unsupported hind margin is coupled with extensive closure of cells, and shortening of outlying branches of veins.

A tribal classification, like any other, can be approached from different directions. Ideally,no doubt, it should be austerely scientific, and express as completely as possible the ancestry and present relationships of the genera. This must always be a matter of opinion. Traditional taxonomic methods of examining as many individual specimens as possible and comparing the results are laborious and incomplete. Professor Theodor's recent paper on the genitalia of Asilidae is full of stimulating observations, but in the end we are left in much the same position as with external, superficial characters. We record resemblances and differences, but every generalisation has its exceptions. Certainly there are some group-characters in genitalia, but I know of no evidence that genitalic characters, or any other that are difficult to see, or which need dissection, are more reliable indicators than external details.

Nowadays numerical taxonomy, with the aid of computers, is being increasingly applied to the formulation of classificatory systems, and the success or otherwise of new methods is judged by the extent to which they confirm traditional classification. Wilkinson (1970) writes: "Methods of numerical analysis are discussed which have given little support to earlier classifications, and have recommended radical changes", whereas Sands (1972) writes: "Where the groupings suggested by the numerical results appeared wrong by conventional standards they have been adjusted to conform to the latter".

As yet computerised numerical methods of taxonomy are in their developmental stage, but it is my personal view that they will prove more useful for analysing data than for synthesising them: i.e. for sorting individuals into species rather than for classifying species into genera, tribes and subfamilies. I think our present classification of Asilidae will remain largely intuitive and utilitarian for a long time to come, perhaps for ever.

The second adjective---'utilitarian'--- is important. In so far as they are not just a source of intellectual satisfaction, all classifications must be useful and, if possible, convenient. Here the very first couplet of Hull's key (1962:25) gives trouble. It seems simple to decide whether the palpus consists of one segment or two, but in most Asilidae the palpi are partly hidden in a mass of hairs at the base of the proboscis. They are usually more or less cylindrical or slightly inflated, but often have a wrinkled appearance, with varying amounts of hairs or bristles. Even after these have been removed it is difficult to say without dissection whether or not a definite suture exists. On practical grounds therefore this is a bad way in which to start a key, particularly the introductory key to the entire work. It may--or may not-- be a matter of theoretical interest. Asilidae being descended from some nematoceran ancestor, the implication is that the single-segmented palp is the culmination of a process of reduction from the multisegmented palp of the Nematocera. The section of the key for one-segmented palpi does in fact include Ommatiini and Asilini, which most workers would accept as the most advanced tribes, but it also includes Leptogasterini, about which there is dispute, as well as several minor tribes. Of course reduction of the number of palpal segments could have taken place more than once.

If this first key were presented as a phylogenetic arrangement it might be appropriate to start off with a palpal character, but there is no suggestion of this. It seems to me, therefore, that the number of palpal segments is too elusive and enigmatic a character to be given such prominence.

While we are on the subject of practical utility in taxonomic characters, let us consider one of Hull's favourite characters, the third antennal segment. His Figs. 1-396 show a fascinating range of antennal structure. Since the

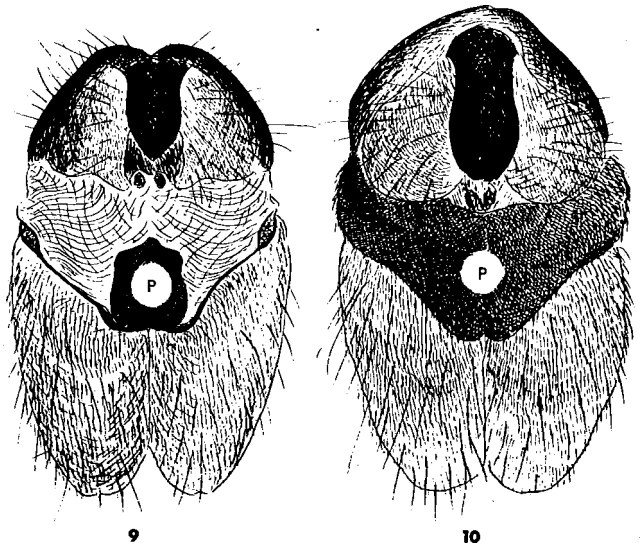
drawings follow broadly along the lines of classification of the family, two things are at once apparent: that while most Asilidae emphasise the first flagellar segment, with the style relatively short, if varied in shape, it is generally characteristic of Asilini and Ommatiini to emphasise the style--which has become aristiform--- at the expense of the first flagellar segment; but that wide variations occur between genera that are otherwise closely alike. Here we are handicapped by the fact that Hull figures only one species of each genus, and so we have no idea of the extent of interspecific variation. But the immediate practical problem, at least to a museum taxonomist, is that the porrect antennae of Asilidae are intensely vulnerable, and sooner or later are usually broken off. Unscientific though this may seem, if the antennae are missing any classification based on them is rendered useless. Moreover Hull himself (1962:5) draws attention to the variability of the antennae, but he still relies upon them at times in his keys: e.g. couplets 5,8,21 of the first key to subfamilies and tribes.

A character discussed by Hull and by other writers, is the state of the prosternum, whether it is completely separated from the pronotum, joined to it by 'arms', or more or less solidly united with it (Figs. 9,10). Like most other recent authors Hull refers to a paper by Clements (1951) which, he says,"... has shown that there is great instability in the character of the prosternum within many groups of asilids", though Hull goes on to say that: "Broadly speaking, the character of the prosternum does help to define the tribes Laphystini and Atomosini because it is universally complete in these groups..." He debates what might be the functional effect of having the prosternum 'floating' in membrane, or fixed immovably to the adjoining sclerites, and comments on its condition in other families of Brachycera.

Clements' paper has been cited by subsequent authors over more than twenty years, but most of them have confined themselves to quoting or paraphrasing the second sentence of his summary: "Examination of the prosternum in all groups showed that too much variation occurs for it to be used as a diagnostic or supplementary character". In my opinion the facts detailed in the paper do not warrant such a sweeping conclusion. The author arrives at it because he tries to distinguish a 'complete prosternum' from one that is 'emarginated', and discovers that the degree of emargination

varies considerably between different genera, for example in the tribe Xenomyzini. He attaches great importance to this fact because he starts from the assumption that the primitive condition is to have the prosternum complete, and that therefore the degree of emargination is some indication of the evolutionary sophistication of the genus.

If the state of the prosternum is used simply as a convenient taxonomic character, without any phylogenetic preoccupations, and applied much more naively, it is of considerable practical utility. My key to the tribes and genera of African Asilidae (Oldroyd, 1963) does this. In particular, the complete separation of a small central sclerite (Fig.9) is a sure way of recognising Saropogonini, in my wide use of this term, and a 'bridged' prosternum (Fig. 10) [whether complete or emarginated in Clements' sense] is a useful supplementary character for Xenomyzini, Stichopogonini, Laphriini and Atomosiini.



Figs. 9,10. Structure of the prosternum, as seen from in front with the head removed: 9, *Neolaparus* (Saropogonini, in my sense of the term), with the prosternum (P) as a small sclerite surrounded by membrane; 10, *Xenomyza* (Xenomyzini) with the prosternum as a large sclerite with 'arms' firmly linked with the pronotum.

A superficial acquaintance with Asilidae shows that they can be broadly divided into four groups, along the lines of the old subfamilies :

ASILINAE --- elongate, grey, bristly, with closed marginal cell and aristiform antennal flagellum.

LAPHRIINAE --- bee-like, with closed marginal cell and rod-like or clavate third antennal segment.

LEPTOGASTERINAE --- 'agrionic', i.e. elongate and excessively slender, and without pulvilli. Marginal cell open.

DASYPOGONINAE --- The rest. Marginal cell open. Flagellum practically never aristiform, and rarely without pulvilli. Otherwise exceedingly diverse in shape and structure.

The first three are fairly clearly defined. Indeed Martin (1968) proposed to remove Leptogasterinae to a separate family, *Leptogastridae*, the 'grass flies', as opposed to the rest, which remained as Asilidae, the 'robber flies'. His detailed arguments did not make it clear why the same treatment should not have been accorded to each of the four subfamilies. A similar step has been proposed in the family Bombyliidae, but the diversity extends much deeper in that family, not only structurally, but biologically as well. Adult Asilidae are remarkably alike biologically, and the only strong divergence in larval habits is that the larvae of Laphriinae live in burrows in wood instead of in the soil like the others. It seems to be a choice between recognising four families, or only one, and it does not greatly matter which we do. The simpler course is to keep them all in one family.

The first three subfamilies divide into tribes with little doubt: Asilinae into Asilini + Ommatiini; Laphriinae into Laphriini + Atomosiini; Leptogasterinae comprising only tribe, Leptogasterini. It is Dasypogoninae that give most trouble. Stichopogonini and Xenomyzini (Damalini) are well segregated, both on head structure --- the former with the eyes widely separated by a a saddle-shaped vertex (Fig. 11) and the latter by the forwardly compressed 'goggle eyes' (Fig. 2) --- and in having the prosternum broadly bridged to the pronotum. The other tribes recognised by Hull have a much less assured status.

Laphystini, Stenopogonini and Dasypogonini correspond roughly to Hermann's 'Untergruppen' Prytaniinae, Eremocneminae and Acanthocneminae, renamed in accordance with the Rule that requires them to be formed from the name of an included genus. Laphystini are a fascinating group, with obvious resemblances to Laphriini, but because of the peculiarly shaped and often not quite closed marginal cell they can be classified as Dasypogoninae. Hull writes (1962:72): "I regard them as an example of convergent evolution, and point further to the fact that of nearly 20 groups placed in the tribe, the members tend to fall into two divisions with the marginal cell either widely open or closed in the margin." He goes on to say that they are " . . . certainly close to the stock which led to the Laphriinae", and in my view this seriously weakens his argument. If the Laphystini were said to be of quite different stock from the Laphriini, or only deceptively convergent, there might be some object in maintaining the distinction.

Laphystini are difficult to key out as either Laphriinae or Dasypogoninae, and they are one of the principal reasons for not bothering about subfamilies, but dividing the Asilidae directly into tribes. Even then it is not easy to delimit the tribe precisely: Hull, for example, includes the genus *Anypodetus* in his key to Laphystini, with the annotation "(Laphriinae)". In my keys I usually give the laphystiine genera a separate entry, but refer to them as belonging to the tribe Laphriini.

Apart from the controversial Laphystini, and the well-established Atomosiini, Hull recognised three other laphriine tribes: Ctenotini, Andrenosomini and Laphrini senus stricto. [The doubling or not of the "i" in tribal names depends on the linguistic dogma of the author]. His Ctenotini comprises four genera which he says are" . . . noteworthy for their elongate, 1-segmented palpus and their blunt claws. All four of these genera have a characteristic row of bristles along the dorsal margin of the proboscis". His key (p. 362) however, immediately separates two of the genera, *Lamyra* and *Stiphrolamyra* which have this row of bristles from the other two, *Ctenota* and *Paractenota*, which do not! Similarly, the key explains that the last two genera have 1-segmented palpi (having previously said that all four have this), and the description of *Lamyra* on p. 365 says "Palpus of two segments. . .", and emphasises this by giving a detailed description of both segments. It is evident, therefore, that Ctenotini is untenable, at least as

here defined. It is possible that these four genera share a common character in a peculiar flange at the base of the proboscis (Fig. 4F), but this, like the palpi, is difficult to see, and is by no means certainly confined to these four genera.

Andrenosomini are more clearly defined, since the genera concerned have the second segment of the palpi curiously flattened and curled into a leaf-shape. Yet *Hyperechia, Proagonistes, Dasyllis* and *Andrenosoma* have little else in common beyond the fact that they tend to prey on aculeate Hymenoptera, and to resemble them. These four genera do not, however, look very much alike, and many other laphriine genera resemble Hymenoptera. It is simpler to treat all Laphriinae as being either Atomosiini --- recognised by the alignment of the veins at the apex of the discal cell, and looking like small sawflies --- or Laphriini. Such characters as those of the palpi are useful in keying out groups of genera.

Stichopogonini and Xenomyzini call for little comment, but they account for only a few genera. In contrast, vast numbers of genera fall into the two tribes Saropogonini and Asilini. My concept of Saropogonini includes 154 genera, and is admittedly a 'dump', which Hull tried to break up, but with small effect. He made little tribes for a number of Australian or Gondwanian genera, following the example of G.H. Hardy, who pioneered tribal classification in this family, and who, from an Australian viewpoint, naturally tended to be very conscious of these 'aberrant' genera. They are aberrant in the sense that they do not classify well with the genera of other regions, and it may well be that they are relicts of ancient stock, like so many groups of austral distribution. I doubt, however, whether a book on a world scale benefits by segregating these genera into such tribes as Enigmomorphini, Thereutrini, Chrysopogonini and Phellini.

This is a basic problem of classification, what to do with aberrant or anomalous taxa. A kind of taxonomic honesty -- or is it tidiness? -- inclines one to sort these out and give them a different name, but the practical effect is too easily to lose sight of them. This is illustrated by Hull's similar treatment of the motley collection of genera that he groups into his tribe Dioctrini. He tries to find common characters, but his first sentence betrays the flimsiness of these: "Here are placed those Dasypogoninae, excepting *Phellus*

Walker, *Damalis* Fabricius, *Laphystia* Loew, *Chrysopon* Roeder and their allies, in which the female ninth tergite is generalised and lacks acanthophorites and spines." But the genera mentioned all fall into other, different tribes, and if they can lack acanthophorites why should this lack suddenly become a character of positive value, uniting the genera of the dioctrini? It is true that *Dioctria* is an anomalous genus, irritatingly so because it is the commonest Asilid in many northern countries, and therefore misleading if taken as a typical Asilid by newcomers to the family. Yet Hull's statement that, except for the Australian *Nerterhaptomenus* the other Dioctrini are 'restricted to the Holarctic region' is simply not true: of the genera in his key *Hermanella* is South African, and *Aplestobroma*, *Pegolabrus* and *Broticosa* were all described from Australia by Hull himself.

Even the Holarctic genera brought together here have little to do with each other. *Molobratia* and *Leptarthrus* are quite dissimilar; though each has a fore-tibial spine these are structurally quite different. *Pritchardia* has nothing to do with *Myelaphus*, or with *Dioctria* either. The only effect of erecting this tribe is to remove a number of genera from the bigger keys, so that they are lost sight of, and their practical identification made difficult.

The tribe Megapodini has a sounder basis. It was erected by Carrera, again to accommodate an anomalous genus, *Megapoda* Macquart, big flies, of gaunt, elongate shape. With it were grouped a number of characteristically South American genera. The status of this tribe is a matter for the consideration of South American asilidologists. Dr. Nelson Papavero has suggested to me that *Neolaparus*, including *Lagodias*, a common and exceptionally difficult genus of the Old World tropics, ought to be removed to Megapodini. Hull is therefore justified in retaining this tribe, though perhaps not in raising it to the status of a subfamily.

Since the time of Macquart (1838) it has been known that certain genera of Dasypogoninae have a spur on the tip of the fore tibia. Hermann named these genera Acanthocneminae, and the spurless genera Eremocneminae, and Hull replaced these incorrectly formed names by Dasypogonini and Stenopogonini respectively. This has a certain practical convenience, except that the spur is easily overlooked, but the genera thus assembled are not a convincing natural group. They differ even in the structure of the spur itself, and

in the manner and extent to which a corresponding outgrowth appears on the basitarsus. I prefer to keep them all together in Saropogonini, even though this results in a long and rather tortuous key to genera. I feel that in this way there is less risk of losing genera between one tribe and another.

My tribe Saropogonini is quite simply recognised, by having the prosternum in the form of a small shield-shaped sclerite, widely isolated by membrane from any contact with the pronotum (Fig. 9). This can always be confirmed by detaching the head, and afterwards sticking this back, with little outward sign of disturbance; in most cases the membranous area can be clearly seen without doing this, since the head is often displaced to one side or the other.

Ommatiini are very distinctive, at least as long as the fringed antennae remain intact (Figs. 12-14) and even without these the bodily structure is distinctive to a practised eye. I have little doubt that this is a valid group, though perhaps not too distantly related to some genera of Asilini such as *Heligmoneura*.

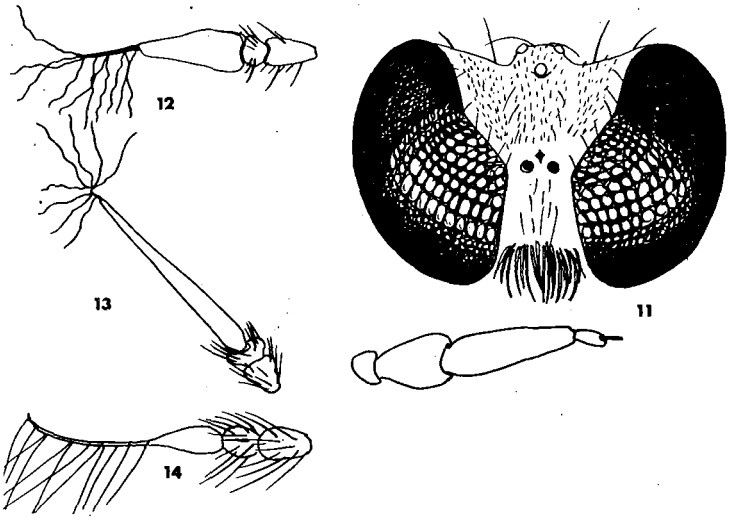


Fig. 11. Head of *Stichopogon* (Stichopogonini) from in front, showing the saddle-shaped excavation of the vertex and frons.

Figs. 12-14. Antennae of three African genera of Ommatiini: 12, *Thallosia;* 13, *Michotamia;* 14, *Ommatius*.

Finally Asilini is a large assembly of 112 genera of mostly grey, elongate, bristly flies. Ironically, the genus *Asilus* sensu stricto, the type genus of the tribe as well as of the family, is very small, and almost restricted to a handfull of Holarctic species. To compensate, there are very large genera such as *Promachus, Machimus* and the *Neolophonotus*-group. The general picture is of a recently evolved group, in active evolution, with a large number of little fragmentations, and a few difficult complexes where generic limits are not easy to define, and subgenera and species-groups abound. If one felt inclined to split up this rather unwieldy tribe, these complexes could be convenient foci, with *Promachus, Heligmoneura, Neolophonotus, Nerax, Machimus* and perhaps *Asilus* itself as centres.

In the present state of classification, Asilidae undoubtedly have an embarrassing number of genera in the big tribes. If one felt an irresistible urge to split the family, I think the first step would be to break them into four, along the lines of the old four subfamilies---Leptogasterinae, Laphriinae, Dasypogoninae and Asilinae--- and then to form new tribes from these. But as I said earlier, the robber flies present so much the picture of a homogeneous family that such a step seems retrograde. Instead, I suggest that attempts might be made to reduce the number of genera by first grouping them into complexes where differences are relatively small. In this family where structural differences abound, it should not be assumed that every structural difference justifies the erection of a new genus. An example of this was the new species from Nepal that I described (Oldroyd, 1964a: 239) as *Oldroydia maculata,* and had subsequently to correct (Oldroyd,1964b: 701) when it became apparent that it was a synonym of *Dasypogon scatophagoides* Walker. The confusion arose because Hull had removed the latter to a new genus *Toremyia,* because of differences in the antennal style, disregarding both the inconvenience of this character, and the many similarities that made it most unlikely that his genera *Oldroydia* and *Toremyia* could really be segregated.

After studying Asilidae for 37 years I feel that many genera could usefully be merged, with beneficial results to tribal classification. This is not to say that small structural differences are always insignificant. The genera *Promachus, Philodicus, Alcimus* and *Apoclea* are sepa-

rated in keys by apparently trivial and indeed variable, differences in wing-venation, yet the whole habitus of each genus is distinctive, and they can be picked out by eye from a mixed box quite easily. It is not suggested that obvious differences should be ignored, but that as far as possible species should be fitted into existing genera, and genera into existing tribes, and the proliferation of new taxa reduced to a minimum.

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