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by

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I regret that I am unable to attend your workshop but hope that I can still contribute in absentia. In the program circulated by Dr. Sabrosky, I am listed as a discussant for the session entitled "Male Genitalia in the Classification of Chloropidae", following talks by Drs. Kanmiya and Nartshuk. Since I have not seen the text of their talks I cannot respond to them. Nor is it likely that I could contribute anything new to discussion of relationships within the Chloropidae, as I have not been working on this family. My contribution to your workshop will be to comment on the male genitalia of Chloropidae from a comparative morphological standpoint, in comparison with the genitalia of other Cyclorrhapha and Diptera generally.

Since I published comments on chloropid genitalia in my 1972 book, I am pleased to note that a wealth of more detailed information has been published, particularly in the major works of Andersson (1977), Nartshuk (1977) and Kanmiya (1983). These works make my 1972 treatment out-of-date on certain points: for instance, Andersson has pointed out that I interpreted the sternites of Apotropina shewelli (Sabrosky) wrongly, the 5th sternite not being absent but forming the first of the asymmetrical sternites. It also appears that the gonites can not be homologized throughout the family, and that the obliquely directed sclerites between the hypandrial arms which I declined to homologize can be interpreted as the gonites or parts thereof (i.e. "pregonites"). All this is progress.

On the other hand these works can be seen as retrograde in that they have failed to follow the lead of my 1972 book in recognizing that the male terminalia of Cyclorrhapha can only be homologized with those of other Diptera on the assumption of continuity in the clasping function. This change in thinking has met with some quite irrational resistance from persons who ought to have known better, and it seems that some dipterists will grasp at any hypothesis, however absurd, which seems to offer justification for retaining the old interpretation that the clasping mechanism of Cyclorrhapha is of tergal origin, differently from that of other Diptera and other insects.

The fact is that it is impossible to provide a consistent and defensible interpretation of the structure of the Orthogenya, the sister-group of the Cyclorrhapha, except by assuming that the clasping mechanism is of ventral origin, as in other Diptera. Most dipterists accept that the ventral claspers of primitive Diptera can be homologized with the gonopods of the 9th abdominal segment, which are normally divided into a basal gonocoxa and apical gonostylus. Formerly I used Snodgrass' terms basimere and telomere for these two articles, but now feel more confident that their homology with the articles of the gonopod is justified.

Chalva's recent finding that the true epandrium (or 9th tergite) is retained in the true Empididae (in his restricted sense) considerably strengthens my interpretation that the clasping mechanism of the Eremoneura is of ventral origin and identical with that of other Diptera. If the clasping mechanism of primitive Empididae is interpreted as of tergal origin, then it must now be assumed (after taking account of Chalva's findings) that in the groundplan of the Eremoneura the epandrium was divided into three separate elements each with different musculature, namely the dorsal plate (epandrium in Chalva's sense), the paired lateral plates and the pair of clasping lobes; meanwhile there is very little left which can possibly be interpreted as representing modified gonopods: either we are driven (with J. F. McAlpine) to postulate that certain unmusculated non-articulated hypandrial processes present in Orthogenya and primitive Cyclorrhapha represent reduced gonopods, or with Andersson to homologize the gonites of

Cyclorrhapha with the gonopods despite inappropriate function and musculature. Something is obviously amiss here, since no comparison of function and musculature with other Diptera is possible on the basis of such homologies.

Hennig's (1976) attempt to salvage the theory of tergal origin by interpreting the clasping lobes as derived from the 10th (instead of 9th) tergite is certainly erroneous, since refuted by several ontogenetic studies. Evidently he had not assimilated the considerable ontogenetic literature published in the last decade of his life. It is not helpful to the progress of science when a respected worker publishes hypotheses which are refuted by information already available. The fact is that the segmental origin of the various structures forming the male terminalia of Eremoneura is not in any doubt, thanks to the very detailed studies of the development of imaginal discs now available, and advocates of the tergal origin hypothesis cannot avoid the absurdity of postulating the derivation of three separate elements from the original epandrium by arbitrarily attributing one or more of these to the 10th segment.

The interpretation which I advocate, that the clasping mechanism is the same in Eremoneura as in other Diptera, entails postulating that the gonocoxae of Eremoneura have been modified by dorsal expansion and partial desclerotization of their inner surfaces. In other Diptera the gonocoxites are closed distally and normally support paired gonocoxal apodemes; but in Eremoneura the gonocoxites are open distally, with their former inner surfaces separated as the sclerites variously termed processus longi, Skleritleiste, interparameral sclerites etc. Primitively these sclerites are paired, but in many Orthogenya and Cyclorrhapha they become fused anteriorly. The sclerite in Chloropidae called "ventral epandrial sclerite" by Andersson is of this origin. The term I now recommend is intergonopodal or intergonocoxal sclerite. The interpretation of such sclerites as derived from the 10th sternite advocated by Hennig (1976) and others is certainly erroneous, since contrary to the ontogenetic evidence that they belong to the 9th segment.

An adequate discussion of these morphological matters is of course hardly possible in a brief unillustrated talk, and I expect that by now some of my audience will have lost track of the argument. Therefore, I have prepared for circulation a summary of how I presently synthesize the data relating to the characterization of the Eremoneura and its two subgroups, the Orthogenya and Cyclorrhapha, and the implications for genitalia homologies. Copies of this are available for interested persons to pick up after this discussion.

The main changes which are required in the terminology used by recent authors on Chloropidae is that the erroneous uses of the terms epandrium and surstyli must be abandoned. The true epandrium (9th tergite) is absent in the Chloropidae, as in all other Cyclorrhapha, and true surstyli (in the sense of articulated lobes of tergal origin) are known to me only in Asilidae. The saddle-shaped sclerite which workers on Cyclorrhapha have misinterpreted as the epandrium is in fact formed by fusion of the gonocoxites across the dorsum. If a term with -andrium suffix is desired for this sclerite, I have suggested periandrium in my 1972 book. The so-called surstyli are none other than the gonostyli.

Of course there are still a few problems regarding genitalia homologies to be solved. In particular, there remains uncertainty as to the homology of the sensory structures called gonites in Cyclorrhapha and parameres by many authors on lower Diptera. These were called paraphyses by Snodgrass. Their homology with the parameres of Coleoptera, as accepted in the Ottawa Manual, is most probably incorrect, and I note that Dr. Ole Saether agrees with me that the term parameres would now be best avoided by dipterists. Saether homolo-

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gizes possibly homologous structures in Chironomidae with the volsellae of Hymenoptera. Andersson (1977) in his chloropid monograph argued against my homologization of the gonites of Cyclorrhapha with the paraphyses of lower Diptera because of their possession of macrochaetae in some groups. This objection seems to me simplistic, since macrochaetae have certainly appeared in the course of evolution on many surfaces where there were none previously. In my opinion the presence or absence of macrochaetae says very little about the homology of structures when considered in isolation, but must be considered along with other factors. Therefore I do not agree with Andersson's argument, although I recognize that the homology of the gonites of Cyclorrhapha with possible homologues in lower Diptera needs further study. Continued use of the term gonite can meanwhile be recommended for taxonomic papers, as no disputed homologies are thus implied.

While I have the attention of this audience of chloropid workers, it may be useful for me to comment on the affinities of the family. In my 1972 book I placed it in the Chloropidae family-group together with the Acartophthalmidae, Carnidae and Milichiidae, and this was accepted as a basis for discussion by Andersson (1977). Subsequently Hennig

(1972) described a new genus of Carnidae, *Neomeoneurites*, whose structure suggests to me that the Carnidae were misplaced and are in fact closer to the Tephritidae family-group. If this is correct, the Chloropidae family-group should be restricted to the Chloropidae, Milichiidae and (more tentatively) the Acartophthalmidae. Since Andersson and Hennig have also accepted that the Chloropidae and Milichiidae are closely related, I was astonished to see that in the system to be followed in the Manual of Nearctic Diptera the Chloropidae have been placed in the so-called Ephydroidea (i.e. Drosophiloidea) while the Milichiidae have been placed in a miscellaneous assemblage called Opomyzoidea. I am not aware of any justification for this placement in recent literature on the affinities of the families of Schizophora, and can only assume that the concept of Drosophiloidea (as Ephydroidea) used in the Manual is a regression to the vague concept predating Hennig's 1958 paper, in which the modern concept of Drosophiloidea was first validated. I hope that specialists on Chloropidae will resist this retrograde feature of the Manual system and not confuse recency of publication with recency of concept.

In conclusion, I wish you every success in your deliberations and hope that mutual illumination will result.

### Note on characterization of Eremoneura, Orthogenya and Cyclorrhapha

by  
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The Eremoneura is a very well characterized group and I see no possibility that the Orthogenya (= Empidoformia) should be grouped with the Tabanomorpha and Asilomorpha, as certain unenlightened colleagues persist in arguing. The male genitalia of these "lower Brachycera" are very similar to those of Bibionomorpha, and I see the formation of a complete sclerotized bridge between the gonocoxites by fusion of the bases of the gonites (= paraphyses, volsellae, "parameres" in sense of the Ottawa Manual) with the gonocoxal apodemes and with each other (forming a sheath around the aedeagus) as a possible synapomorphy between the Bibionomorpha and "lower Brachycera". Hennig (1976) argued that this bridge could be homologized with the hypandrial bridge of Orthogenya and some Cyclorrhapha (e.g. Platypezidae), but I doubt whether there is any such synapomorphy since the bridge in the latter does not involve the gonocoxites or gonites. According to Chalvas's studies the closest approximation to the groundplan of the Orthogenya is shown by *Hormopeza* (Empididae), and groundplan conditions for the Eremoneura can be inferred by comparing this with primitive Cyclorrhapha.

Eremoneura can be characterized in terms of modifications of the larval structure, wing venation, male and female genitalia. In the male genitalia the groundplan modifications are: (1) gonocoxites expanded dorsally (but the true epandrium still retained in the groundplan, as in *Hormopeza* and most Empididae in Chalva's restricted sense); (2) gonocoxites not closed distally (with separate bacilliform sclerites on inner surfaces of gonocoxae) - this partial desclerotization of the gonocoxae is the origin of the processus longi of Calypterae etc. = Skleritleiste of Empididae (which I previously called interparameral sclerites when fused anteriorly - now the most appropriate terms are intergonopodal or intergonocoxal sclerites) - that these sclerites are part of the gonocoxae is especially clear in *Hormopeza* in which the gonocoxae are rather projecting; (3) separation of the paired (gonocoxal) apodemes from the gonocoxites (precise groundplan condition unclear, but in neither of the subgroups are the apodemes attached to the gonocoxites as in other Diptera - probably separation of these apodemes was a result of the partial desclerotization of the gonocoxae already stated); (4) hypandrial arms fused above base of aedeagus (i.e. Hennig's bridge, which is well developed in Platypezidae as well as in Orthogenya, so probably belongs to the groundplan although lost in many Cyclorrhapha); (5) hypandrium with pair of posterior processes (confused with gonopods by McAlpine, but they are not muscled and never articulated, and the structure of *Hormopeza* is not compatible with this interpretation); and (6) 10th tergite lost (not a very useful character, since the same has occurred independently in other groups). In the female genitalia the most obvious groundplan modification is the complete loss of the sclerites of the 9th segment shown by all

Orthogenya and all Cyclorrhapha except for a few genera of Syrphidae with strongly modified ovipositors in which a furca is secondarily developed again. Another apomorphy is that the cerci have only a single article (but this reduction has occurred independently in other groups). The wing venation modifications are of course the 3-branched media (m3 fused with m4) and apical closure of the anal cell.

Turning to the two subgroups, while the Orthogenya are more primitive in most respects I see the following as apomorphous: (1) in the male genitalia the paired apodemes are attached to the hypandrial bridge (a condition which led Hennig to argue that the apparent hypandrium of Orthogenya really represented fused sternite and gonocoxites, as in Bibionomorpha - but this leads to some highly implausible consequences when applied to *Hormopeza*, in which the paired apodemes are not attached to what are obviously the gonocoxites - I conclude that the fusion postulated by Hennig did not occur, but it was the attachment of the apodemes which changed); (2) in the female there is only a single spermatheca. The above characters suggest that the Atelestidae belong in Orthogenya, and that periandrium formation in this group must be a parallelism (not synapomorphy) with Cyclorrhapha.

The Cyclorrhapha are characterized by the following further modifications of the male postabdomen and genitalia: (1) loss of the epandrium (= 9th tergite) and fusion of the gonocoxites across the dorsum (the proper term for the resulting saddle-shaped sclerite, if a term with -andrium suffix is desired, is periandrium, not epandrium) - since all sclerites present in Cyclorrhapha as well as a reduced true epandrium are present in *Hormopeza*, it is evident that the clasping mechanism in Eremoneura is the usual ventral one and that the replacement theory implied by the conventional application of the terms "epandrium" and "surstylus" in literature on Cyclorrhapha is erroneous - loss of the true epandrium also occurs (through parallelism) in some Orthogenya, including Atelestidae and Hybotidae, according to Chalva; (2) fusion of the paired (gonocoxal) apodemes to form the unpaired "aedeagal apodeme" (a separate sclerite, not attached to the hypandrial bridge as in Orthogenya); (3) ejaculatory apodeme free (i.e. without muscular connection to the body wall); (4) hypopygium circumversum condition, resulting in looping of the ejaculatory duct over the hind gut and crossing of the lateral tracheal trunks (partly reversible in groundplan, as in Platypezidae, see my 1972 book) - 8th segment rotated through 180°, hypopygium through 360°; (5) inverted 8th tergite (in ventral position) reduced to narrow band. The female genitalia are characterized (in the groundplan) by 2 of the 3 spermathecae sharing a common (branching) duct. Groundplan modification of the wing venation is the two-branched radial sector (r4 + 5 not branched), but this is not very useful due to parallel reduction in other groups.