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THE NOMENCLATURE OF THE PARTS OF THE MALE HYPOPYGIUM OF DIPTERA NEMATOCERA, WITH SPECIAL REFERENCE TO MOSQUITOES

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It has long been recognised that the structure of the tip of the male abdomen is of the greatest importance in the classification of insects, and an enormous amount of work has been done in figuring the organs in different species. Unfortunately, however, the greatest diversity and confusion exists in the naming of the different parts, and nowhere is this more apparent than in the mosquitoes. The terms used for the lepidoptera have been applied to these insects in altogether different senses from those in which they were originally used, and, moreover, have been used even in different genera of the family Culicidae for structures which are clearly not homologous. The writer hopes in the notes which follow to indicate terms which can be generally adopted for all mosquitoes, and as far as possible those have been chosen which are applicable to other Diptera, if not also to other orders of insects. Since, however, the mosquitoes are amongst the most generalised Diptera in regard to genital structure, it must not be expected that the same terms will all apply to the highly specialised Brachycera and Cyclorrhapha. Reasonable allowance has been made for the claims of priority, but it has not been considered advisable to follow a rigid rule in this respect, and the name judged most suitable has been chosen in each case.

Of the many writers who have concerned themselves with the genitalia of mosquitoes, the only one who appears thoroughly to understand the subject is Christophers (1915). This author has given an accurate analysis of the parts in *Anopheles*, and has also pointed out the existence of a very remarkable and extremely

important phenomenon: that in *all male mosquitoes*,* *shortly after the emergence of the adult, the tip of the abdomen undergoes torsion through an angle of 180°*, so that the parts which are morphologically ventral become dorsal, and *vice versa*. It is probably failure to appreciate this fact that has led to most of the confusion in regard to the naming of parts; certainly such a failure has caused Brolemann (1919), the latest writer on the subject, to speak of the genital chitinisations as the 'cylindre perianal,' and the anal sclerites as the penis.

Good as Christophers' work was, it dealt only with *Anopheles*, where all the parts are not well developed, and so requires supplementing and slight modification.

Before proceeding further, it will be well to state the now universally accepted fact that the hypopygium of mosquitoes, † as of all but the more specialised metabolic insects, is composed of four distinct parts ‡:—

- (1) A more or less continuous chitinous ring, representing the tergite and sternite of the ninth abdominal segment.
- (2) A pair of appendages of the ninth segment, more or less ventral in position (except secondarily in mosquitoes).
- (3) Chitinised pieces surrounding the anus.
- (4) Chitinisations of the genital tube, as opposed to the main body wall, which forms the other three parts.

We will discuss each of these elements in some detail.

(1) THE CHITINOUS RING OF THE NINTH SEGMENT. This is spoken of by Lepidopterists as the *tegumen*,§ the term having been introduced by Buchanan White (1878) and its use modified by P. H. Gosse (1883). Although in a great many insects, including

* Females are not so affected, but the phenomenon is not confined to the males of Culicidae. It occurs also in the males of Psychodidae (in *Plebotonus* and probably others) and Dixidae, and also in the Tipulid genera *Molophilus* and *Rhypholophus*.

† The present writer, in common with some others, has frequently spoken of the 'genitalia.' This term, however, should perhaps be confined to the chitinisation of the genital tube. *Hypopygium* is on the whole the best, used in the sense in which Snodgrass (1904) employed it, to include the four elements distinguished above; it is, however, not very appropriate for the Nematocera where the structures are terminal, not ventral as they are in Brachycera and Cyclorrhapha. Other terms in use by different writers are *male armature* and *copulatory apparatus*, but these seem less satisfactory.

‡ In a few cases the eighth abdominal sternite undergoes special development in the male, constituting a fifth element, but the occurrence is so rare that it may be dismissed with a mere mention. In any case there is no ambiguity about the term eighth sternite.

§ Not to be confused with the *tegmen* of the Coleopterists, which has an entirely different signification.

mosquitoes, it forms a continuous ring, yet this is not always the case, and even where it is, the ring is very much narrowed at the sides, leaving differential dorsal and ventral portions between which it is often possible to find traces of a suture. There seems, therefore, no need for the term *tegumen*, and it will be preferable to speak, as most writers on the hypopygium of Diptera now do, of the *ninth tergite* and *ninth sternite*.

The true ninth tergite is ventral in position in mosquitoes, as explained above. It is generally more or less distinctly bilobed, the lobes bearing bristles or spines, but its form varies greatly in different genera. I have used (1914) the morphologically incorrect term 'ninth sternite' for the whole structure; its lobes are the *setaceous lobes* of Felt (1905) and the *basal appendages* of Howard, Dyar and Knab (1912). This last term is inadmissible since the structures are not appendages. No objection can be raised to Felt's term, except that it is unnecessary. I propose to call these parts the *lobes of the ninth tergite*. The fact that they have sometimes been referred to as the lobes of the ninth *sternite* need cause no confusion, because the true ninth sternite is not usually lobed. These lobes have not been used as much as they might be in specific and even generic descriptions. Their most primitive form is seen in *Megarhinus regius*, where the tergite is broad, and without any emargination at the tip. In *Anopheles* and *Aëdomyia* the tergite is barely discernible and carries no bristles. In *Aedes* a pair of lobes are well developed, each nearly as long as broad, and bearing a row of spine-like bristles. The Sabethini show considerable specific differences, but the lobes are generally much more elongate than in *Aedes*, though sometimes shorter. In *Culex* they are broad and short and the terminal bristles are more hair-like. In some forms (e.g., *Uranotaenia pallidocephala*, *Armigeres obturbans*) the bristles are absent.

The ninth tergite is well developed and obviously distinct from the sternite in most families of Nematocerous Diptera, and often, particularly in the genus *Tipula*, exhibits most diverse specific modifications. In Cyclorrhapha, through the atrophy of the eighth or pregenital segment of Awati (1915) it is apparently the eighth: it is very large and folded back under the abdomen, covering the anal and genital parts. In *Phlebotomus* it is almost completely divided

into two elongate lobes, which Newstead (1911 *b*) has called the inferior claspers.

The true *ninth sternite* has been incorrectly spoken of by me (1914) as the ninth tergite, and equally incorrectly by Leicester (1908) as the sur-anal plate. It exhibits fewer modifications in the Culicidae than does the tergite, being usually represented by a narrow strip of chitin. In some *Anopheles* it is apparently absent; in *Culex perfidiosus* it is greatly enlarged; in a few species of *Aedes* (sub-genus *Aedes*) it has developed lateral processes, and in some forms it is strongly emarginate at the tip. It usually bears a few bristles about the middle, and in *Armigeres obturbans* is chitinised only at the sides and round these bristles.

The ninth sternite is well developed in most Limnobiidae, and in *Trichocera*, but in Psychodidae and some Mycetophilidae it is not distinguishable; in many other Mycetophilidae, in Bibionidae and in *Tipula*, it is very large and forms a single piece with the basal joint of the forceps (see below). In Cyclorrhapha it is said by Awati (1915) to be absent, but may possibly be represented by his vesiculum or by the editum of Newstead (1911 *a*). However, it is very difficult to homologise the part of the Nematocera with those of the Cyclorrhapha, and it is beyond the writer's intention and competence to do so.

(2) THE APPENDAGES OF THE NINTH SEGMENT. In all mosquitoes, as well as in the majority of the more primitive Diptera, the ninth segment bears a pair of two-jointed* appendages, which articulate with the ninth sternite, usually at its attenuated sides. Appendages of the ninth sternite occur in other orders of insects; they are universal in Lepidoptera, where the term *harpagones* was proposed for them by Buchanan White (1878); by P. H. Gosse (1883) they have been styled *valves*, and by some Lepidopterists *harpes*. The first and third of these terms have been used in varying and contradictory senses by writers on Culicidae, but never for the appendages of the ninth sternite; they are not in use by other Dipterists, and it is inadvisable that they should be retained. The term *valves* is quite inappropriate, at least in regard to the Diptera, and it also must be rejected.

* Three-jointed if the terminal spine is reckoned as a joint.

The term *forceps* (*forcipules* of the French writers, *Zange* of the Germans) has frequently been employed, and will be useful when it is desired to speak of the whole appendages.

(a) *The basal joint.* The homology of this piece is uncertain. By many it is regarded as simply a specialised part of the ninth sternite, and there is much to be said in justification of this view. As stated above, in many Nematoceros Diptera, including most Mycetophilidae and Bibionidae, the part cannot be distinguished from the ninth sternite, though it is quite possible to argue that this may be due to a secondary fusion. The apical part of the sternite in these cases has usually a median furrow or slit which may indicate either incipient division or incomplete fusion. Another point to be noted is that in some cases where the ninth sternite is apparently separate from the basal joints of the forceps, these latter are connected at their bases ventrally (e.g., *Trichocera*, *Macrocera*). In Limnobiidae the sternite and basal joints of the forceps are usually well separated.

In view of the uncertainty as to the exact homology, and pending further investigation and discussion, it will perhaps be as well to avoid using the term 'basal joint of forceps.' This is the more desirable since other terms are in use by students of Nematocera. Snodgrass (1904) proposed *pleuron*, while Dyar and other writers on the Culicidae speak of it as the *side-piece*. Both these terms are good, but Snodgrass's suggests the implication that it is derived from a separate pleural piece analagous with the thoracic pleura: perhaps a correct assumption, but as yet unproven. *Side-piece* is more non-committal, and is widely used by writers on Culicidae. There seems, therefore, to be no occasion for replacing it.

This part is subject to many important modifications in the different genera of the family. In most it has the form of a hollow chitinous tube, widely open at the base, especially on the inner side, and tapering more or less to the tip. Sometimes, however, the chitin is discontinuous on part or the whole of the inner aspect of the tube, where the wall may be formed of thin membrane only. *Anopheles* and *Chaoborus* have the tube complete, or almost so; some lacunae of chitinisation appear in some of the early Culicine genera, notably *Megarhinus*, the final stage being reached in the *Aedes* group, of which it is highly characteristic. Here the side-

piece forms a *lower flap** (ventral in actual position) and an *upper flap* (dorsal) connected on the outside by chitin and on the inside by thin membrane, which extends right up to the tip.

The apical and basal lobes of the side-piece, of which so much use has been made in the classification of the *Aëdes* group by Dyar (1918) are developments at the apex and base of the lower flap of the side-piece. The terms are appropriate, and I do not propose to alter them, but it may be worth while to point out that the basal lobes of *Megarhinus* seem to be developed from the upper flap of the side-piece, and further that the basal lobes in *Uranotaenia*, *Theobaldia*, etc., which have the chitin of the side-pieces tubular, may not be homologous with the basal lobes of *Aëdes*. The ventrally-directed, *sub-apical lobes* of *Culex* seem to be an independent development, as they can be traced back to *Theobaldia*, where they originate as simple hairy knobs quite independent of the basal lobes. The latter have disappeared in *Culex*, the sub-apical lobes having probably taken on their function, whatever that may be.

In the *Aëdes* group a characteristic modification of the base of the *upper flap* of the side-piece occurs, which in the great majority of species has become practically a distinct organ. For this part the term *harpe* was used by Felt (1905), though that author had very imperfectly studied the homologies, and used the same term for the anal chitinisations of *Culex*. Howard, Dyar and Knab (1912) adopted Felt's terms in restricted and differing senses, and spoke of the parts now in question as *harpagones*. Both these terms, however, are unfortunate and misleading, especially the latter, which, as has already been stated, was originally applied by Buchanan White to the main clasping organs of the Lepidoptera, which are probably equivalent to the side-pieces. The name *harpe* was first introduced by P. H. Gosse (1883) for an internal appendage of the side-piece (*harpago*), and there would, therefore, seem to be some justification for the use Felt made of it in the Culicidae. However, I consider that the *harpe* of the Lepidoptera (in the sense of Gosse) is more likely to be the equivalent of the second joint of the forceps of Diptera, than of the special organs in

* It will be well to avoid the terms *dorsal* and *ventral* as far as possible to save possible confusion.

consideration which are only found in the genus *Aedes*. Moreover, the term has been used so inconsistently in the Culicidae that its retention is undesirable without strong reason.

The term *claspette* was used in a loose way by Felt, apparently to cover any appendage, basal or apical, of the side-pieces, other than the clasper. Since the special organs of *Aedes* are undoubtedly homologous with the basal lobes of some forms (if not of all), there can be no objection on morphological grounds to the use of the term *claspette* for them, and no confusion will result from its re-introduction, as it has not been in general use. I propose, therefore, to make use of it for the harpagones (Dyar) of *Aedes*, and for the similarly derived structures of *Taeniorhynchus*, without necessarily intending to imply a strict homology between these two. The same name may also be applied to the parts in *Anopheles* which Christophers (1915) has spoken of as the harpagones, since it seems most probable that they are, as he suggests, homologous with the claspettes (harpagones) of *Aedes*. The *claspette spines* of Christophers would be better known as the *basal spines*, since they are not borne by the claspettes and may well be homologous with the basal lobes of *Aedes*. The term *basal lobes* I propose to reserve for the structures at the base of the lower flap of the side-piece in *Aedes*, and for the hardly differentiated organs of some other genera (*Megarhinus*, *Theobaldia*, etc.).

Brolemann (1919 *b*) speaks of the claspettes as *gonapophyses*, and regards them as appendages of the tenth tergite, but this is merely owing to his fundamental misconception as to the anus and the genital opening. He has further been led to the erroneous deduction that the claspettes are primitive organs which have disappeared in *Culex* and other genera, whereas they are unquestionably special developments (most probably arising quite independently) in *Aedes*, *Anopheles* and *Taeniorhynchus*. I prefer not to use the term *gonapophyses*, as it is a loose one used by different writers to indicate appendages of the ninth or tenth segment or of the genital tube.

Before leaving the side-pieces, it will be necessary to notice one other structure which has escaped the attention of most writers on the subject, Christophers excepted. This is an internal prolongation of the base of the side-piece on the lower (anal) side, variously

developed in different genera. I propose to term it simply the *apodeme*. Its importance will appear later on.

(b) *The second joint*. This I have spoken of as the clasper, and this term seems to be in fairly general use, though some writers, Christophers for example, have used it to include the basal joint or side-piece also. I do not think this fact need prevent its retention in the sense in which I have employed it. There has never been any doubt as to its homology throughout the Nematocera, unless perhaps in one or two aberrant species of *Aedes*, but its modifications are extreme. On this account I object to the term *clasp filament*, which has been widely used by Howard, Dyar and Knab: the structure is only 'filamentous' in certain groups, the description being absurdly inapplicable to such elaborate developments as are found in *Sabeithes*, and many *Aedes*.

Berlese (1906) calls this part the *mesostylus*; Snodgrass (1904) the apical appendage, and de Meijere (1919) the *stylus*. The first two of these are not sufficiently expressive; no objection need be made to the third, but *clasper* seems to me preferable as having been in more general use by the English writers. In those Diptera (such as the majority of Limnobiinae and Mycetophilidae) where it is double it will be useful to speak of the *upper* and *lower claspers*, though it is possible that one part may have originally been a terminal joint, or a mere lobe of the other. This does not apply to mosquitoes. The position of the plane of articulation of the clasper is important. It is vertical, or nearly so, in *Culex*, almost horizontal in *Aedes* (sub-genus *Ochlerotatus*).

The *spine* or *claw* of the clasper is best spoken of as such (*claw* being rather better than *spine*). It has been regarded by Brolemann (1919) as a third joint of the forceps, but this is not established. It may be *terminal* or *sub-terminal*, or rarely absent.

(3) THE ANAL CHITINISATIONS. By most writers the anus of insects is regarded as opening at the tip of the tenth abdominal segment, though Berlese (1906) recognises an additional segment near the base, and so counts the anal segment as the eleventh, while Keilin (in conversation) considers the anus to be situated on an appendage of the ninth, and does not admit a separate anal segment. At present, I believe that the majority in this case are right, and I therefore propose to follow the usual custom and speak

of the plate or plates dorsal to the anus as the *tenth tergite* or *tergites*, and those ventral to it as the *tenth sternites*.

In many insects the tenth tergite bears a pair of appendages (the anal styles, stylets or cerci), but this is not the case in the males of any Culicidae. Both tergite and sternite, however, are generally divided completely into two parts. The *tenth tergites* have not, so far as I am aware, been noticed by any previous writer* on the family, though they are quite well developed as two simple plates in most of the genera, particularly in *Theobaldia* and *Culex*. Apically they are in contact with the tenth sternites, basally with the ninth tergite. Owing to the torsion, they, of course, occupy the most ventral position in the hypopygium.

The *tenth sternites* are conspicuous in most Culicidae, and are the parts miscalled *harpes* by Howard, Dyar and Knab and 'bras peniens' by Brolemann. Their true nature is shown in any lightly macerated specimen by the fact that the rectum is attached to them (and to the tenth tergites); furthermore, they nearly always bear some minute bristles, which illustrates their cuticular origin. Though this is not true of all other insects, bristles seem never to occur on the genital chitinisations of Diptera.

A condition of the anal segment very similar to what is found in the Culicidae occurs in the Cyclorrhapha. In *Glossina* the halves of the segment have been spoken of by Newstead (1911 a) as *superior claspers*, but the true homology of these parts has been pointed out by Awati (1915), whose opinion I can confirm. In *Phlebotomus*, however, Newstead (1911 b) calls the anal segment the sub-median *lamellae*, and uses the term *superior claspers* for the forceps. This is no doubt owing to his having overlooked the torsion, which is as regular a feature of *Phlebotomus* as of the Culicidae, and is one of the points of agreement indicating a connection between the two groups. In Mycetophilidae, Bibionidae and Cecidomyiidae the anal segment usually has a different form, the tergite being divided into two hairy lamellae resembling the cerci of the female, while the sternite remains entire.

The most primitive conditions of the anal segment is probably that in which both the tergite and sternite are simple. This is the case in *Chaoborus*, though here the tenth tergite is fused on to the ninth. A very similar condition occurs in the Lepidoptera (see

* They are indicated in some of my published figures, and also by Brolemann, but have not been specially mentioned.

below) and also in Chironominae. In *Anopheles* there is often practically no chitinisation either of tergite or sternite, the whole segment being membranous; in some species two ill-defined bars of chitin represent the sternite. The same is true of *Aëdomyia*, and in these cases Christophers' term *anal lobe* is appropriate.

In other Culicidae the form of the anal segment varies little, except in *Culex*, where the sternites develop crowns of spines and in many cases a strong *basal arm*, projecting upwards and more or less surrounding the aedoeagus. In their primitive condition (as regards the Culicidae) the tenth sternites probably bore apically a few strong bristles or teeth (as in *Theobaldia* and *Taeniorhynchus*); the number of these has greatly increased in *Culex* to form the crown of spines, while in *Aëdes* they have entirely disappeared. In addition to these spines there is nearly always a patch of a few very minute hairs, doubtless sensory in function, at the sides near the tip; these occur in *Aëdes* as well as in *Culex*. In all cases where they are well developed, the sternites have a downward projection in the form of a strip of chitin extending up to and articulating with the lobes of the ninth tergite. (figured by Felt, 1905, p. 465). Whether this is a primitive or secondary structure I am unable to say. It does not appear to exhibit any characters which can be made use of in classification, and it will, therefore, be unnecessary to name it.

Dyar (1918) speaks of the anal sternites (*harpes*) as evolving from a simpler to a more highly developed form, and regards their absence in *Anopheles* as primitive. It is quite certain, however, that the reverse is true, and that this absence is due to degeneration.

(4) THE GENITAL CHITINISATIONS. As in the case of most other insects, the genital tube of mosquitoes opens between the ninth and tenth sternites, and its apical part, with one or more invaginations, is more or less heavily chitinised. These chitinisations have been called collectively by Felt (1905) and Howard, Dyar and Knab (1912) the *unci*, though in the case of *Culex* these writers have also spoken of parts of them as *harpagones*.

The inapplicability of the latter term has already been explained. The name *uncus* was first introduced by P. H. Gosse (1833) for the 'posterior part of the dorsal arch of the eighth segment' of the Lepidoptera, and has been in use ever since for the same structure,

which, however, was incorrectly described by Gosse as belonging to the eighth segment. It has since been homologised by Rothschild and Jordan (1904) as the tenth tergite. The term *unci*, therefore, ought not to be used for structures belonging to the genital tube. Brolemann's term 'cylindre perianal' is, of course, out of the question, being founded on a misconception.

Christophers (1915) and Awati (1915) have adopted the term *theca*, which was first introduced by Wesché (1906) for the 'penis sheath' of certain Diptera, chiefly Cyclorrhapha. I reject this, however, as it is not by any means in general use among students of other groups, and the homology of the pars in Cyclorrhapha is still very uncertain. The alternative term *adminiculum* of Westhoff (1882) has not often been adopted. The whole structure is often spoken of, perhaps correctly, as the *penis*, but I consider that this term would be better reserved for the actual intromittent organ when present. On the whole the term which seems open to the least objection for the chitinised parts of the genital tube is *aedoeagus*, which, according to Sharp and Muir (1912) was introduced by Foudras in 1859. It is in general use among Coleopterists in the sense indicated, but, unfortunately, has been employed by Pierce (1914) and other Lepidopterists in a much more restricted sense, to indicate the intromittent organ. I consider that Sharp's usage is the one that should be followed, and propose to adopt the name *aedoeagus* for the *ensemble* of chitinous structures of the genital tube of Diptera, thus exactly reversing Pierce's use of the terms penis and aedoeagus.

The apparent correspondence between primitive Diptera and primitive Coleoptera in the details of structure of the aedoeagus is remarkable, and comparable modifications have also been described for the Anoplura and Mallophaga. There is, of course, an immense divergence between the more specialised species, but in the more primitive forms, among which may be included the majority of the Culicidae, it is possible to distinguish the following parts:—

(a) *Basal plates*. These are a pair of chitinisations of the sides of the genital tube lying within the ninth segment and often extending back into the eighth. They doubtless serve for the attachment of muscles. Although generally overlooked, they have been mentioned by Dyar (1918) as *ligaments* and by Brolemann

(1919 *b*) as *apodèmes aliformes*. The name *basalplatte* was proposed by Verhoeff (1893) for the corresponding structure in the Coleoptera, where, however, it usually forms but a single piece. I propose to adopt this name, using it in the plural, as the structures are apparently always paired in the Culicidae. Sharp and Muir (1912) prefer the expression *basal piece*. Waterston (1914) and Cummings (1916), on the other hand, use basal plate.

The basal plates vary much in size, attaining their maximum in *Culex* and *Theobaldia*. They articulate near their inner extremities with the apodeme of the side-piece, and it is noteworthy that the size of the apodemes varies inversely with that of the basal plates. In very many cases (conspicuously in *Theobaldia longiareolata*) there is a definite fusion between the basal plate and the apodeme, so that it is impossible to say where one ends and the other begins. In *Uranotaenia* this fusion is for almost their entire length. At their outer ends they articulate in a notch situated near the middle of the parameres, and they are also in close contact, though never fused, with the tenth sternites.

(*b*) *Parameres*. These are paired structures which, as just mentioned, articulate with the basal plates. They are nearly always present, though in varying degrees of development, being very minute in *Aëdomyia*, and perhaps absent in *Anopheles*. They were formerly referred to by Dyar and Knab (1909) (in *Culex*) as the fourth plate of the harpagones; more recently by Dyar (1918) as the first uncal plate. Brolemann (1919 *b*) calls them *trigonapophyses*. Berlese (1906), Snodgrass (1904) and de Meijere (1919) use the term *gonapophyses*.

The term *parameres*, which I have adopted as most suitable, was proposed by Verhoeff (1893) for the Coleoptera, and has been adopted by Waterston (1914) and Cummings (1916) for the Siphonaptera and Mallophaga respectively. While in these different orders the structures may not be strictly homologous, they are certainly similar in position and appearance. Sharp and Muir (1912) prefer the expression *lateral lobes*.

In some cases, though not in any mosquitoes, the parameres are fused with one another and with the basal plates. When this is so, Sharp's term *tegmen* may aptly be applied to the whole structure. This seems to be the condition in the genus *Molophilus*.

(c) *Mesosome*. Lying between the parameres is a more or less complicated body which has been incorrectly styled the *unci* by Howard, Dyar and Knab (1912), or the second, third and fourth uncal plates by Dyar (1915). Though apparently composed, especially in *Culex*, of one or more pairs of distinct organs, a close examination will nearly always show that it is really only one piece, more or less elaborately lobed. The very handy term *mesosome* was proposed by Waterston (1914) for the structures lying between and distal to the parameres of the Philopteridae (Mallophaga), and I propose to make use of it. I think it is preferable to the *median lobe* of Sharp and Muir (1912) since the structure often bears many lobes or divisions.

The mesosome is a thickening of the walls of the distal part of the aedoeagus. The chitin seems generally to be disconnected on the upper (apparent dorsal) side, but the lateral portions are generally, if not always, connected by a chitinous *bridge* (a good term used already by Dyar) on the side nearest the anus. This bridge varies much in width in different species, being extremely broad in *Aedes* subgenus *Ochlerotatus*, and very narrow in many species of *Culex*. When the halves of the mesosome are connected by chitin on the dorsal and ventral sides of the genital tube, the bridge nearest the rectum may be called the *lower bridge*, and that furthest from it the *upper bridge*. The terms dorsal and ventral would be ambiguous, and had best not be used. The two bridges are both distinct, though narrow, in *Culex*. In the higher members of this genus there are two or more fairly distinct parts of the mesosome, which seem to be developed mainly or entirely on the upper wall of the tube, and probably do not indicate an invagination of the tube. When a second invagination is present* the terms *endomere* and *telomere* have been used by Waterston (1914) and Cummings (1916) for the proximal and distal portions of the mesosome. I have not been able to satisfy myself, however, that any such division occurs in the Culicidae, even among the more complicated forms.

The structure of the mesosome is of great taxonomic importance, and there is probably no other single organ of the body which gives better clues to the true phylo-genetic relationships of the species.

* The first is at the base of the parameres.

It is beyond the intention of this paper to discuss its modifications in detail, but it may be mentioned that in *Culex* the bridge or bridges are nearly or quite basal, the part beyond them being drawn out into horns or spines, usually on the upper side of the tube. In *Aedes*, on the other hand, as in many other genera, the lower bridge is almost or quite apical; as it is also much broader, the mesosome of these forms is necessarily practically a rigid structure, and is only capable of slight extension by the action of the parameres, conjunction with the female being effected mainly by the aid of the mobile forceps. In *Megarhinus* the lower bridge occupies a middle position, and in this as in some other points this genus should probably be considered among the most primitive of the family.

The true genital structures of *Anopheles* are very different from those of other Culicidae, and are difficult to homologise. It is almost impossible to distinguish parameres, basal plates and mesosome as can be done in the other genera of the family. The first two appear to be represented by a small single piece no larger than the paramere of *Aedomyia* (see fig. 2, c). The mesosome is Christophers' *theca*, but it is of a very different form from that of any of the other genera. A very careful study of cleared and floating specimens of some of the more generalised *Anopheles*, such as *A. plumbeus* or *A. argyrotarsis*, shows that it approaches nearest to the simple form seen in *Ochlerotatus*, with a very broad lower bridge. In most species, however, the chitin has become definitely tubular and the remarkable and characteristic *leaflets* have been developed at the tip.

The structure of *Chaoborus* is also very different from that of the Culicinae, and here there would seem to be no definite aedocagus. There is only one pair of chitinous organs at the base of the side-pieces, occupying a vertical position and possibly to be regarded as developments of the side-pieces themselves. A similar condition occurs in the Chironomidae (excepting Ceratopogoninae), and in both cases is most probably retrogressive. It is possible that a connection may be indicated between the Culicidae and Chironomidae through *Chaoborus*, which, indeed, would also seem likely from a study of some other organs.

Hardly anything is yet known as to the precise function of the different parts of the hypopygium, but one point which is clear from

a study of macerated specimens of *Culex* may be mentioned, as it is of some general interest. The parts of the aedoeagus (see Edwards (1914)) are observed in microscopic preparations in two different positions relative to one another. In one, the position of rest, the halves of the mesosome lie close together, project tailwards, and are partly covered by the parameres. In the other, probably the position of use, the parameres are folded back and the halves of the mesosome either divaricated from the bridge outwards or bent downwards on to the anal sternites. A comparison of specimens in these two positions (the examination should be made in clove oil under a binocular microscope) will show that in the first the upper bridge of the mesosome lies proximally to the lower, and both are almost in the line of the longitudinal axis of the body, the aperture of the genital tube thus being closed. The folding back of the parameres has the effect of pulling back the upper bridge of the mesosome, so that it and the lower bridge lie in a plane vertical to the body, and at the same time divaricating the halves of the mesosome (which lie distal to the bridges and are not connected by membrane), and turning them downwards. The result is not only the genital tube is opened, but that the lower bridge, or the whole mesosome presses on the tenth sternites and thus closes the anus, probably at the same time transmitting some stimulus by touching the minute sense-hairs on the tenth sternites. A quite analogous condition has been described by Waterston (1909) in the Siphonaptera, but I have not seen anything approaching it in other genera of mosquitoes.

The accompanying diagram (fig. 1) will help to explain the

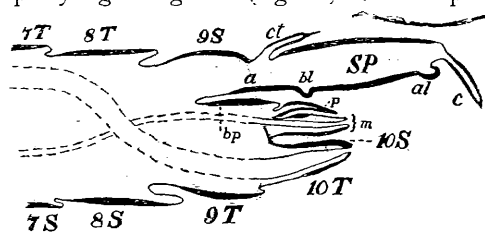


FIG. 1

Ideal section through tip of abdomen of an *Aedes*. The thick lines represent chitinisations, the thin ones membrane. Note the wide membrane between the 8th and 9th segments, which allows of the torsion. 7T—10T, seventh to tenth tergites; 7S—10S, seventh to tenth sternites; SP, side piece; c, clasper; ct, claspette; bl, basal lobe; al, apical lobe; a, apodeme; bp, basal plate; p, paramere; m, mesosome.

foregoing analysis of the Culicid hypopygium. It represents an ideal longitudinal section through the tip of the abdomen of an *Aedes*, this type being chosen as offering the maximum development of all the structures. All the parts shown are, of course, not actually in the same vertical plane, and the claspettes and parameres are shown dorsal to their true position for the sake of clearness. The course of the rectum and ejaculatory duct is indicated by dotted lines, since it is not quite certain what happens to the internal organs after the torsion. If this diagram be compared with one given by Cummings (1916, p. 688) for the Mallophaga, it will be evident at once that there is a striking similarity in many respects. Camera lucida drawings are also given of the aedoeagus of *Megarhinus*, *Ochlerotatus*, *Aedomyia* and *Theobaldia* (fig 2, A-D), in order to show the principal types of mesosome.

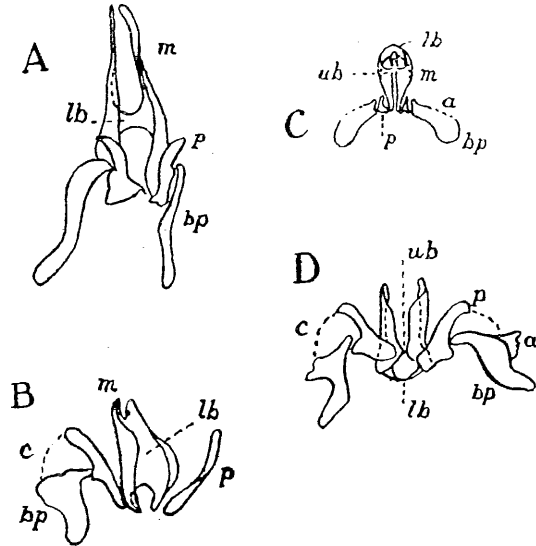


FIG. 2

Aedoeagus of different Culicidae: A, *Megarhinus (Toxorhynchites) regius* (Tennent); B, *Aedes (Ochlerotatus) waterhousei* (Theo.); C, *Aedomyia squamipennis* (Arrib.); D, *Theobaldia annulata* (Schrank). a. position of attachment or fusion of apodeme with basal plate; bp, basal plate; p, paramere; m, mesosome. ub, upper bridge, and lb, lower bridge of mesosome; c, membrane connecting the outer edge of the paramere with the basal plate.

To sum up, a table is also given shewing the chief terms which have been used by different writers on the Culicidae, and for comparison, the equivalent terms used by Newstead (1911 b) for

Phlebotomus and by de Meijere (1919) for the *Tipulidae*. The last-named author compares his nomenclature with that of Berlese, Snodgrass and Westhoff, so that it will be unnecessary to add their terms to this table; reference may be made to de Meijere's work.

In conclusion, I wish to express my indebtedness to Dr. D. Sharp and Capt. J. Waterston for much kind assistance on difficult points.

Proposed Terms	Felt, 1905	Dyar, 1918	Brolemann, 1919	Newstead, 1911	de Meijere, 1919
Ninth tergite ...	Setaceous lobes	Basal appendages	Ninth sternite	Inferior claspers	Ninth tergite
Ninth sternite ...	—	—	Ninth tergite	—	Ninth sternite (proximal part)
Side piece ...	Basal joint of clasp	Side piece	First joint of forceps	Superior clasper (basal joint)	Basal joint of forceps (part of ninth sternite)
Basal lobes ...	Claspette	Basal lobes	Verrue basale	—	—
Apical lobes ...	Claspette	Apical lobes	Saillie apicale	—	—
Claspettes ...	Harpes	Harpagones	Gonapophyses of 10th sternite	Intermediate appendages	—
Apodeme ...	—	—	—	—	—
Clasper ...	Second joint of clasp	Clasp filament	Second joint of forceps	Superior clasper (second joint)	Stylus (terminal joint of forceps)
Tenth tergites ...	—	—	—	} Submedian lamellae	Tenth tergite
Tenth sternites ...	} Harpes (<i>Culex</i>) } Harpagones (<i>Aedes</i>)	Harpes	Bras penien		Tenth sternite
Aedoeagus ...	Unci ?	Unci	—	—	—
Basal plates ...	—	Ligament	Apodème aliforme	} Intromittent organ	—
Parameres ...	—	First plate of unci (<i>Culex</i>)	Trigonopophyses		Gonapophyses
Mesosome ...	Harpagones (<i>Culex</i>)	Second to fourth plates of unci (<i>Culex</i>) Unci	Cylindre perianale	Genital filament	Penis

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