Suggested short title:

BIO-SYSTEMATICS OF SOME CERATOPOGONIDAE

SYSTEMATICS OF THE FORCIPOMYIINAE (DIPTERA: CERATOPOGONIDAE) WITH ECOLOGY OF CERTAIN QUEBEC FORMS

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GENERAL INTRODUCTION

Most people know the ceratopogonid midges as "no-see-ums" and "sandflies" and have encountered them while on a fishing trip or on a holiday to the seaside, countryside or to mountain regions. The annoyance they give from their bites invariably engenders an abrupt fall in morale and produces an instant strong desire to be elsewhere. As Kettle (1962) has put it, "one midge is an entomological curiosity, a thousand can be hell!"

The term "sandfly" is inappropriate for these insects as it leads to a confusion of the group with the true sandfly Phlebotomus (Psychodidae) and certain blackflies (Simuliidae). "Midge" or "biting midge" is the preferred term since it is in common usage for the Ceratopogonidae in English-speaking countries (Lee, Reye and Dyce, 1963; Reye, 1963). It generally stands for the whole family rather than strictly for the biting members of the family.

Biting midges as a whole are little known except where they become a menace to human welfare and health. Their economic and medical importance are becoming increasingly better known as more attention is being paid to them. Their potential as vectors of diseases (virus, nematodes) among mammals and amphibians, and as pollinators of tropical economic plants like rubber and cacao, is being looked into but to date, no work has been carried out on these insects as vectors of diseases of insects and plants, an area of study of equal importance if not more so.

The subfamily Forcipomyiinae contains many species of economic and medical importance. Saunders (1959), for example, found two species of *Proforcipomyia* as pollinators of cacao in Trinidad and three other species of *Proforcipomyia* and one species of *Thyridomyia* as possible pollinators of the plant. Warmke (1951, 1952) found that the Para rubber tree, *Hevea brasiliensis* Muell. Arg., in tropical America is mainly pollinated by the Forcipomyiinae of which the genera *Atrichopogon* and *Forcipomyia* were the most frequently found in *Hevea* flowers. Members of medical importance in the subfamily belong mainly to the genus *Lasiohelea*. Several man- and cattle-biting species of *Lasiohelea* s. str. have been recorded but only one species, *townsvillensis*, has been definitely identified from male genitalia as belonging to the group. Others, that have been correctly identified as belonging to *Lasiohelea* s. str., suck blood from amphibians. For example, on frogs, *velox* (Winnertz) acts as a vector of *Icosiella neglecta* Diesing (Desportes, 1941, 1942) and *fairfaxensis* Wirth acts possibly also as a vector of frog filaria (Pechuman and Wirth, 1961), and on the toad *Bufo asper* Gravh., Yuen and Chan in Yuen (1962) found a blood-sucking species of *Lasiohelea*, as yet unidentified, infested with the parasite *Icosiella innominata* Yuen. More recently, 1965, a new species, *Dacnoforcipomyia anabaenae* Chan and Saunders, of the genus *Lasiohelea*, was determined to be a biting species on man in Singapore. According to Downes (1958), there are two records of *Atrichopogon* species biting mammals but these require confirmation.

It is regrettable that the systematics and ecology of the Forcipomyiinae, in fact of the Ceratopogonidae as a whole, are poorly understood and little known. The taxonomy of the Forcipomyiinae has not progressed very much beyond the traditional stage of arduous identification and classification of species from adult stages alone. Saunders (1956, 1959, 1964) and Ewen and Saunders (1958) have approached the subject from a new angle by incorporating immature stages with adults in the classification and revision of the group, and have thus opened a new and more precise taxonomic avenue to the systematics of the ceratopogonids. However, descriptions of all stages have hitherto been mainly qualitative and do not provide room for the possibility of separating sibling species.

Very few non-systematic biologists truly understand what systematics is and very often the subject is confused with taxonomy, an inclusive branch of this discipline (Simpson, 1961). Systematists are often looked upon as dilettante biologists who know nothing but the identification and classification of organisms. Systematics is looked upon as a specialization or restricted field of biology rather than as a discipline or a way of looking at biology. Clearly, it should be pointed out that systematics is a unifying science, in the same way as evolution is a unifying biological theory accounting for the diversity of life on earth. It embraces all branches of natural sciences and attempts to correlate and coordinate all known knowledge relating to organisms, be this knowledge on individual species or populations or groups of genera, families, etc., so that natural phenomena and life may be expressed in an orderly, organized and intelligible manner. Simpson (1961) has attributed to it a proper status when he remarked, that it is "a science that is most explicitly and exclusively devoted to the ordering of complex data, and in this respect it has a special, a particularly aesthetic, and almost a superscientific place among the sciences".

At the present time systematics is evolving with the changing trends and philosophies in biological concepts and has become sufficiently sophisticated to embrace the expression of the theory of evolution in a practical way. This contrasts with the past when the theory of evolution had no effect upon taxonomy and it was "impossible to tell by a man's taxonomic work whether he believed in evolution or even knew about it" (Blackwelder, 1962). In classificatory aspects of systematics, conventional methods of taxonomy are being increasingly supplemented by modern computerized methods of data storage and processing and of mathematical analysis of correlations of characters and of functional relationships (Munroe, 1964). The "old systematics" which is gradually demising, has given birth to the "new systematics". Non-morphological characters are now being looked upon as of equal importance, if not more so, than morphological ones since they add a whole new dimension to the taxonomic picture of a species. In the light of progress in this field, the systematics of the Forcipomyiinae must necessarily take a new direction. Taxonomic information, once past the identification stage, must be accumulated in large quantities and this is best achieved by combining the quantitative approach to the qualitative one. Quantitative data will enable us to investigate more adequately, using correlation analyses, the functional relationships that exist in the phylogeny of species.

Results reported here on the study of the Forcipomyiinae contain detailed quantitative information used in descriptions of new species and is made available with the aim of providing future systematists with a basis for separating sibling species with the use of discriminant functions and for working out systematic relationships. An attempt has also been made for the first time to work out the phylogeny of the Forcipomyiinae and their geographical distribution from the viewpoint of establishing their phylogeny.

For a long time animal populations have been known to regulate their numbers, i.e., maintain "a population level which does not differ from a long-term average by more than one or two orders of magnitude" (Macfadyen, 1963) but the mechanisms bringing about their control are still not fully understood although Klomp (1964) has tried to break them down into four main categories. Many theories have been advanced by many authors as reviewed by Thompson (1956), Solomon (1957) and Nicholson (1958) and theoretical (mathematical),experimental and field evidences have been accumulated through the years to explain the natural phenomenon of regulation of animal numbers. The general conclusion appears to be that the mechanisms of control of population size in nature are very complex and vary enormously with different species and under different circumstances. The factors responsible are many and intricate but, despite our lack of experience in this field, they can be analysed and measured (Macfadyen, 1963).

It is not the intention here to review the different theories on population regulation that have been propounded by various authors, notably Thompson, Andrewartha and Birch, Nicholson, Solomon, Milne and recently Morris and his followers, nor is it the intention here to show which of these is the most acceptable and tenable. Each theory has its merits and demerits and cannot fully explain the fluctuations of all animal populations under all circumstances primarily because of the complexity and diversification in the properties of living organisms. The student ecologist can often become biased and prejudiced through trying to follow and accommodate a particular theory or, for that matter, any system of thought, and thus become convinced that that particular theory is most acceptable, e.g., the Red Chinese, indoctrinated and inculcated with the philosophy of Marxism since childhood, truly believe that communism is the only solution to world peace and prosperity, and similarly, American democrats believe the democratic way is the right way to world problems. The same student can also become confused when he approaches the same subject from different angles and sees new lights which he would otherwise not perceive if he had stuck to the same approach. After weighing the several theories philosophically and scientifically he is left, if he had been considering them with an open mind, with the scientific approach to the problem and that is to assemble observational and experimental data and deduce from these, _a posteriori_, the phenomena operating in the system and then formulate a working principle for the natural phenomena involved.

The present ecological study of three ceratopogonid members in a pond community at Morgan Arboretum constitutes a preliminary quantitative study of these species in all their stages through a reasonable sampling period and it shows that such a quantitative approach, though in the present form incomplete, can provide a body of information on the behaviour of insect numbers. It is unfortunate that due to lack of man-power and time, complete life table studies could not be done. Life table studies could however have been done on a single species, say, the predator _Palpomyia slossonae_ (Coquillett), but this, no matter how complete, would not have provided information on, and an insight into, the intimate interactional relationship between predator and prey species, the effect of interspecific competition with other predators, the types of ceratopogonid adult emergence in inland freshwaters, etc. Richards (1961) has pointed out that "a complete life table tells what happened in a particular year but, as it stands does not enable prediction of future changes", so that "any attempt to make detailed deductions from even several consecutive years of life tables will involve study of the biology of the more important parasites and predators in some detail" since Nicholson (1954, 1958) has shown and emphasized that the behaviour of parasites and predators toward their host or prey at different population levels, is more important than the percentage parasitism or predation in a particular year. A study of the parasites and predators will therefore provide a better understanding of population dynamics of any particular species than studies on a single species. It is devoutly hoped therefore that this present study be extended in great detail and if possible, encompass more species in the community, so that a rounded picture of an ecological community can be understood. This quantitative approach to insect population dynamics is important because we lack, at present, the necessary precise data for working out the dynamics of a whole community.

SYSTEMATICS

I. INTRODUCTION

A. SYSTEMATIC HISTORY OF THE FORCIPOMYIINAE

Until 1917 the family Ceratopogonidae was considered a subfamily of the Chironomidae (Tendipedidae). Early attempts at classifying the family in a natural way are reviewed in a later section on the phylogeny of the Forcipomyiinae.

The subfamily Forcipomyiinae first received its name from Lenz (1934) and the use of the name was subsequently recognized and followed by Enderlein (1936) and others. Wirth (1952) included two genera in the subfamily, notably, Forcipomyia and Atrichopogon. The systematic history of these two genera antedates that of the subfamily.

Forcipomyia, a large genus of the subfamily Forcipomyiinae, first received this name from Mergele (in Meigen, 1818) who, though he did not define it, tried to distinguish it from the all-embracing genus Ceratopogon which then included a host of blood-sucking and other midges. Kieffer (1901) was the first to assign generic characters to Forcipomyia but could not accept the genus - "Je ne puis admettre ce genre". Goetghebuer (1914) used the name but later (1920-1921) confused it with the old name Ceratopogon and still later (1923) went back to Forcipomyia. Edwards (vide Saunders, 1924) was the only author to use the name consistently. Since in general usage the name Forcipomyia is attributed to Meigen (1818), who first published it as a rejected name proposed by Mergele, it is best for the sake of uniformity to accept the name as of this date. Besides, Hardy (1960) has petitioned the International Commission for Zoological Nomenclature to validate Forcipomyia Meigen, 1818, by placing it on the Official List of Generic Names in Zoology.

Being very large, the genus Forcipomyia has from the start presented difficulty to early systematists on this group. Various attempts were made to subdivide it by splitting off or creating new genera, subgenera, or groups - all attempts except Saunders' (1925) being based on adult characters. Saunders (1956), in his revision of the genus, showed all previous attempts based on adult characters to be inadequate and, by incorporating characters of immature stages (both larval and pupal) in conjunction with those of the adults, divided the genus into eight subgenera: Forcipomyia, Proforcipomyia, Warmkea, Caloforcipomyia, Metaforcipomyia, Synthyridomyia, Thyridomyia and Trichohelea. He considered Lasiohelea and Pterobosca to be closely related to Forcipomyia but not close enough to lose their generic status. Of all the systems, Saunders' seems most natural and has been adopted by Tokunaga and Murachi (1959) who have further included Lasiohelea and Pterobosca as subgenera on the basis of adult characters. In the same year they added yet another subgenus, Neoforcipomyia, chiefly on the basis of male genitalia, and, pending discovery of immature stages, erected four provisional new subgenera, designated as "A", "B", "C", and "D", also based on adult characters. Saunders (1964), on discovery of the early stages, endorsed their action with regard to Lasiohelea and Neoforcipomyia but refrained from committing himself with regard to Pterobosca which still remains unknown except in the adult female stage. In the same paper Saunders (loc. cit.) recognized Kieffer's genus *Lasiohelea* as "an association of subgenera of *Forcipomyia* having in common an elongated second radial cell in the wing", and included three subgenera, viz. *Lasiohelea*, *Neoforcipomyia* and *Warmkea* under the term "*Lasiohelea* complex".

Chan and Saunders (1965) erected yet another subgenus when the early stages of a man-biting species in Singapore was discovered by Chan in 1961. The females of this species were indistinguishable from those of *Lasiohelea*, in fact conspecific with *L*. *stimulans* according to Wirth (pers. com.), but the subgenus is clearly separable on characters of the larva and male genitalia.

In the present study the writer finds Saunders' (1956) system of classification based on all stages, not only taxonomically sound but also scientifically accurate besides being most natural. He therefore follows this method and by so doing substantiates the soundness of the approach and extends it further to include new species of this group and a new subgenus, *Schizoforcipomyia*.

Atrichopogon, the other large genus of Forcipomyiinae, was, like *Forcipomyia*, originally included in the rag bag genus *Ceratopogon*, and known mainly in the adult stages. Contributions towards the taxonomy of the genus came chiefly from Kieffer (1925) who worked on the French species, Edwards (1926) on the British, Goetghebuer (1923, 1934) on the Belgian, and Malloch (1915) and Johannsen (1931) on the North American. Wirth (1952) published an extensive account of the Californian species and in 1956 erected a new subgenus, *Meloehelea*, for species which attack meloid beetles and which possess an upcurved proboscis. Kieffer (1913) had previously erected _Kempia_, as a subgenus of _Dasyhelea_, and another, _Gymnohelea_ (Kieffer, 1921) on adult characters which are rather indistinct and unsatisfactory, _Atrichopogon_ adults being notoriously difficult to separate (Edwards, 1926; Nielsen, 1951; Wirth, 1952, 1956a; Ewen and Saunders, 1958).

As attention by entomologists became increasingly focussed on the biting midges due to the economic importance of the group, a number of workers concentrated on a study of the immature stages. Of these studies, the main contributions came from Lenz (1933, 1934) and Mayer (1934, 1955) on the immature stages of the European species of _Atrichopogon_, and from Thomsen (1937) and Boesel and Snyder (1944) on the American species. The descriptions given were unfortunately very brief and from the morphological point of view of little value. The first accurate and detailed descriptions came from Nielsen (1951) on eight Danish species, and an equally excellent account, by Ewen and Saunders (1958), on the revision of the genus with descriptions of 19 new species, mostly Canadian, followed seven years later. Ewen and Saunders (1958) reduced all previous subgenera to one subgenus, _Atrichopogon_ s. str., and retained Wirth's _Meloehelea_ as tentatively valid but subject to further confirmation from early stages other than _meloesugans_, the only species described. Tokunaga (1962) and Tokunaga and Murachi (1959) described species from Micronesia and Ryukyu Islands but only from adults.

B. ON THE APPROACH TO TAXONOMY

As taxonomy becomes more sophisticated with the application of symbolic logic, the setting of theory to classification (Woodger, 1937, 1948, 1952; Gregg, 1954; Beckner, 1959), and the use of statistical methods for evaluating systematic relationships (Sokal and Michener, 1958), modern taxonomists cannot remain insensitive to the evolutionary changes in this field.

A common practice of the taxonomist, still widely used, is the habit of describing new species in an almost entirely qualitative manner. Descriptions in many cases are very brief, and where measurements are given, they are limited to a very few characters (e.g. length of insect, wing length of adults and tarsal ratios for Forcipomyia) and almost always based on a single specimen. The inadequacy of such a qualitative approach is clearly reflected in the all-too-frequent occurrence of synonymy in the group. For example, Forcipomyia (Forcipomyia) fuliginosa (Meigen) has been shown by Wirth (1956) to have at least 27 synonymies from examinations of numerous specimens of both sexes collected from N. America, S. America, West Indies, Africa, Asia and Australia; F. (Neoforcipomyia) eques (Johannsen) to have at least seven synonymies, etc.

Such a qualitative approach using a single type specimen in descriptions is indicative of the basic concept of species which the taxonomist holds, and this is none other than the most widely held concept - the typological species concept. Taxonomists who hold this concept fail to understand the true nature of species. According to this concept which originated from the idealistic philosophy of Plato and the modifications of it by Aristotle, the vast observed variability in nature has no reality and only the eidos (type) has objective reality. Thus this concept of the morphologically defined species, when translated into practical taxonomy, means the description of a species on the basis of a single specimen, the type or "archetype" of Simpson (1961). Such a typological-morphological concept is obviously incompatible with evolutionary thinking (Reiser, 1958; Mayr, 1963) since it treats the individuals of a species as an aggregation of inanimate objects, a singularly inappropriate treatment for a reproductive community. Moreover it is highly misleading in cases of polymorphic diversity within a species or of morphologically extremely similar (sibling) species.

1. Morphological similarities in different species

a. Sibling species

The use of the purely typological-morphological species concept fails when applied to sympatric populations which have virtually no morphological differences (sibling species) but have all the characteristics of good species (genetic difference and reproductive isolation). Sibling species are very common among insects, especially the Diptera, Lepidoptera, Orthoptera and Hymenoptera (Mayr, 1963) and often, as in the case of _Drosophila_ (Dobzhansky, 1961), exhibit no morphological differences even in adult male genitalia. A re-evaluation of the importance in taxonomy of the adult male genitalia which offers one of the most reliable taxonomic characters in the identification and classification of species therefore seems appropriate.

In the Ceratopogonidae the form of the parameres, aedeagus and the structure of the claspettes are basically fairly constant at the generic level and in the Forcipomyiinae at the subgeneric level as well but these are often clearly variable and highly modified at the specific level. Saunders (1956) has successfully utilized (in part) this fact in dividing the genus *Forcipomyia* into eight subgenera and Tokunaga and Murachi (1959) have relied heavily upon the male genitalia in assigning *Lasiohelea* as a subgenus of *Forcipomyia* and in erecting the subgenus *Neoforcipomyia* and two other *Forcipomyia* subgenera ("B" and "C"). Their correct assignment of *Lasiohelea* and *Neoforcipomyia* has been confirmed by Saunders (1964) from evidence of immature stages. Snodgrass (1957) has pointed out the great variability of the claspettes in Diptera and believed that they could be used as reliable characters in the separation of species. However, a problem arises in the separation of sibling species having superficially identical genitalia. Here, separation is possible on the basis of differences in habits, ecology, physiology, pathogenecity, parasites, commensals, symbionts, host preferences, as well as on cytology, biochemical analysis and breeding tests but such studies are highly impractical to the taxonomist who has to deal with many species. In such cases, the biometric approach, whether based exclusively on metric characters or any type of multiple-character analysis, appears most practical and recommendable and has been used successfully in studies on *Drosophila pseudoobscura* and *D. persimilis* (Reed and Reed, 1948), *Etheostoma nigrum* and *olmstedti* (Stone, 1947), *Boloria* species (Petersen, 1947) and *Everes* species (Lorkovic, 1942). There is no reason why the approach should not be extended to the Ceratopogonidae. Since the human mind cannot distinguish imperceptible differences in combinations of characters through multiple summated judgement while the use of mathematics can, the use of discriminant functions (Bigelow and Reimer, 1954; Stanley, 1963) should be employed in the separation of sibling species.

2. Morphological differences in the same species

a. Within population variations

Species of the same population have often been described as different species on morphological differences due to age, sex, season and individual variability (polymorphism and polyphenism) but when they are found to belong to the same interbreeding population despite these differences, they are sunk into synonymy. Such morphological differentiations without acquisition of reproductive isolation necessitates a decision as to species status to be based on a broad evaluation of the species in question.

Morphological differences due to age and sex can be easily solved by rearing the early stages right through to adults. It is unfortunate that there is still a tendency among systematists of the Ceratopogonidae to describe new species, reclassify and revise the various groups by basing their evidence solely on adult characters. Although a convenient and practical classification may be obtained on adult characters alone, particularly from the male genitalia, such a classification cannot be as natural as it could be without showing the evolutional relationship between adults and immature forms and from the evolutionary stand-point, such an approach is evidently inadequate. This explains why it is so necessary to describe a species in all its stages. Seasonal variability, as far as is known, has not been observed in the Ceratopogonidae but it behoves taxonomists on this group to take note of it when performing their trade.

Individual variability which may be entirely genetic or due to nongenetic modification of the phenotype caused by local environmental conditions, is a very common phenomenon among insects. Among the Ceratopogonidae, individual variability in adults of the same sex of the same species is hardly distinguishable by the human eye but measurably distinct in all species where extensive measurements have been done. Size variation among individuals of the same age within a population is often great, especially in species with sexual dimorphism. The problem may thus arise when an individual or specimen of a species is found to be unusually large or unusually small due, for example, to overfeeding or to starvation or to sexual dimorphism, and to have measurements lying outside the range of its typical population. Would the quantitative approach using the discriminant function in separating sibling species be effective in ascertaining its correct assignment to the same species? The answer is decidedly yes. Individual variation in size in a population is often very great but the ratios of measurements taken of sclerotized parts do not vary much. Most Forcipomyiinae larvae for example may vary considerably in overall length among individuals of the same age but their head capsules which are sclerotized do not vary significantly in size and proportions, and ratios of measurements made from the head capsules give even smaller variations. The quantitative approach therefore has great practical taxonomic value in species determination.

b. Between population variations (geographic variation)

Morphological differences occur not only within populations but also between populations of the same species. Such differences among spatially segregated populations of a species very often are as great as between species and sometimes even as great as between genera

(Mayr, 1963).

Geographic variation is very widespread in insects as is evident from Hubbell's (1956) review paper, and other papers like those of Rensch (1943) and Park (1949) on beetles, of Michener (1947) on Hoplitis albifrons, of Lorkovic (1953) on Erebia and of Sacca (1953, 1956) on Musca. In the Ceratopogonidae Kettle (1950) has shown from incompletely analysed data, that there are two seasonal races of Culicoides impunctatus Goetghebuer in Scotland. The two resulting populations differ in their vertical and horizontal distribution and in their sex ratio.

Where geographic variation is not visible it is in most cases due to insufficient study. Adequate biometric analysis has often revealed geographic variation where it is otherwise not apparent (Gotz, 1959), e.g., even in the morphologically notoriously uniform genus Drosophila (Stalker and Carson, 1947; Prevosti, 1954; Teissier, 1958). According to Mayr (1963), lack of geographic variation is attributed to (i) limited species range, (ii) panmictic condition of the species population, (iii) stable phenotype due to developmental homeostatisis, (iv) stable genotype due to genetic homeostasis.

Since geographic variation is a universal phenomenon, it is of great practical taxonomic interest to the working systematist. His main concern should be centred on characters which are geographically variable. These include any character, external or internal, morphological or physiological (Huxley, 1942; Mayr, 1942). In insects, of the external morphological characters, size is probably most subject to variation; other important characters are the surface of the sclerotic covering, such as sculpture and scales of the wings and patterns of coloration.

Of the internal morphological characters, little is yet known but in well studied cases they are just as great as external ones (Mayr, 1963). Cytological evidence shows that much intraspecific variation occurs in chromosome structure (Dobzhansky, 1961) and that the presence and frequency of inversions, the fusion of chromosomes and the existence of supernumeraries are all subject to geographic variation (Mayr, 1963). Modern approach to taxonomy should therefore be directed also to studies on internal anatomy and cytology.

Thus geographic variation again demonstrates the invalidity of the typological concept of species.

C. APPROACH IN PRESENT STUDY

The weaknesses of the approaches used so far in the systematics of Ceratopogonidae are: (i) classification, identification and descriptions of new species, based solely on adult characters; (ii) descriptions of new species practically entirely qualitative, and even if somewhat quantitative, based only on a single specimen, seldom on a large number of specimens; (iii) descriptions of new species when based on all stages usually too brief and almost entirely qualitative; (iv) classification of higher categories in different groups based on different criteria, without reference to, and comparison of, the status of the taxa involved (see section on "Reclassification of the Forcipomyiinae"); (v) approaches based on the typological concept fail to distinguish species that are morphologically identical (sibling species) and fail to relate morphologically different individuals (due to differences within and between populations) to the same species. It is the writer's confirmed opinion that descriptions of new species in all taxonomic work should be (a) done on all stages, (b) adequately quantitative and (c) fully illustrated.

In the present study a practical taxonomic application of the biological species concept is made in descriptions of new species of the Forcipomyiinae and in redescriptions of some species, and systematic relationships between species are evaluated by means of statistical analyses and between groups by comparative morphology of all stages and by other criteria.

Every new species is treated in this study as a population or populations showing genetic continuity and not as an individual or an aggregation of inanimate individuals and population variations are considered real and the type (average) an abstraction in the sense that it alone does not describe fully the species. Each species is defined on the basis of means, standard deviations and standard errors of characters of ten specimens measured for each stage. Such a quantitative approach has the following main advantages: (i) it enables descriptions to be scientifically (i.e. statistically) precise and accurate; (ii) it provides a means whereby sibling species can later be separated by the use of discriminant functions; (iii) it enables a statistical treatment of systematic relationships between species as well as between groups; (iv) it reduces synonymies to a minimum if not perhaps removes them entirely.

It must be pointed out that so far real difficulty in separating closely related species has not arisen with the immature stages, thus supporting Saunders' (1959) claim that "there can be no mistake of specific identity once the early stages are described and figured". Although Saunders' statement still holds it does not exclude the possibility that sibling species do occur in the Ceratopogonidae and that genuine difficulty will arise with the discovery of immature stages of more species either described or new. As a matter of fact, difficulty has already arisen with a few very closely related species, e.g., between *Neoforcipomyia saundersi* n. sp. and *N. crinita* Saunders, between *Proforcipomyia clara* n. sp. and *P. ingrami* Carter (1919) , between *Trichohelea nicopina* n. sp. and *T. brevis* Johannsen, between *Trichohelea grandis* n. sp. and *T. comis* Johannsen, between *Forcipomyia swezeyana* Tok. and Mur. (1959) and *F. swezeyanaadfinis* n. sp. and between *F. bipunctata* Goetghebuer and *F. bipunctatapropinqua* n. sp., where many morphological characters overlap and where distinction depends on differences in one or two characters.

New species are described only when all stages (adult, larval and / or pupal) are available. The solitary habit of some species excludes the possibility of obtaining all stages in large numbers and very often only a single larval or pupal specimen can be obtained through funnelling or direct observation of the substrate. Where the number of specimens of all stages are insufficient for a statistical treatment, or where one of the immature stages is lacking, or where specimens are too damaged for measurements, measurements are made of whatever material is available. Descriptions based on limited measurements are considered preliminary and should be supplemented and further substantiated, and species thus described are subject to redescriptions when adequate material is available.

For all descriptions given here, as many characters as are essential in, and appurtenant to, each description, are figured.

It is the writer's opinion that the primary criterion of species rank of a population should be reproductive isolation since the degree of morphological difference displayed by a natural population is a by-product of the genetic discontinuity resulting from reproductive isolation. In this study, allotropic populations of ceratopogonids treated, having ecological and other similarities are considered as likely belonging to the same species - their minor morphological variations being considered as geographic. To avoid systematic confusion they are described as new but descriptions are subject to confirmation through breeding tests, etc. Morphological differences among sympatric isolated populations on the other hand can be used as a good yardstick in the evaluation of the taxonomic status of sympatric species since sympatry of natural populations indicates reproductive isolation.

II. MATERIAL AND METHODS

A. MATERIAL

Stages of all species herein described came in part (a) from Wallace Way in Singapore, in part (b) from Gunong Pulai in Johore (South Malaya) and in part (c) from Morgan Arboretum, Macdonald College, Quebec, Canada. The exact location of each species is given under the type specification following description.

B. METHODS

1. Collection

Eggs and immature stages of Canadian and Malaysian species were obtained from samples of decaying wood, decaying vegetation (e.g. grass, leaves, twigs), algae and bryophytes (mosses, liverworts, lichens) growing in damp or moist situations, e.g., on soil, rocks and wood, collected in the field by hand, with a spoon or with a knife. Malaysian Trichohelea species were obtained from samples of watery detritus in treeholes, holes in stumps of bamboo shoots, leaf-axils of banana plants, pineapple and aroid leaves, by means of a long glass pipette. Samples collected were placed into polythene bags or into tins and brought to the laboratory for examination under a binocular microscope.

Extraction of immature stages by Berlese funnel as recommended by Saunders (1959) removed larvae only. Eggs and pupae, which remain attached to the substratum, were obtained by visual examination of the materials under a binocular microscope. Fine needles were used to separate the materials, portion by portion. This method, though time-consuming, has a positive advantage in that the substrate so handled remained suitable for use in subsequent rearing of larvae. Eggs and early larval instars were removed from the substrate with a wet No. 2 camel-hair brush, and introduced into petri dishes containing their original substrate for rearing or into vials containing 70% alcohol for storage.

Extraction by floatation using $MgSO_4$ was found relatively unsuccessful.

2. Rearing and maintenance in the laboratory

Larvae were in all cases successfully reared and maintained on their original substrate, after the method proposed by Saunders (1959). Larvae were isolated one per petri dish and their development noted at regular intervals of 12 hours. The substrate in each dish was replenished when food supply became depleted.

Saunders' (1959) method of rearing larvae on artificial cultures was also tried but was not found to be as successful as the above simpler method. In artificial cultures, factors such as unsuitable substrate, wrong pH, presence or absence of other microflora or microfauna, beneficial or inimical to the larvae of the species reared, may have accounted for this lack of success.

Adults that emerged from these rearings were kept alive using the method described by Chan and Saunders (1965).

3. Killing, storage, and examination techniques

The techniques used in the killing, storage and examination of all stages of all species are mainly those of Saunders (1959) and Wirth and Blanton (1959). Larvae were killed by boiling them in a little water contained in a 2" x ½" tube held over a strong flame of a bunsen burner. This extends the whole insect including the pseudopods and anal papillae. Living pupae were killed directly by immersion in 70 per cent alcohol. Adults were killed after they had assumed full coloration and their integument hardened one or two days after emergence, by touching them with an alcohol-wetted camel-hair brush or microspatula and then immersing them in a tube of 70 per cent alcohol.

All stages were stored in 70 per cent alcohol. Prior to storage air was expelled from pupal exuviae to prevent them from collecting near the mouth of the storage tubes. This was accomplished by immersing exuviae in a storage tube half filled with alcohol and pressing them against the inner wall of the tube with a camel-hair brush until all air bubbles were removed.

Preparations for microscopic study were according to Wirth and Blanton's (1959) method. Specimens were cleared in lactophenol for at least one day but for male genitalia they were better cleared in 10 per cent warm KOH for a few minutes. For examination, measuring and drawing under the microscope, the sloping cover slip technique according to Saunders (1959) was used.

III. TERMINOLOGY

The terminology used for the adults (male and female) is a modification of Tokunaga and Murachi's (1959) while that used for the immature stages is original and introduced for the first time in conjunction with quantitative measurements of all important taxonomic characters.

The body length for all stages, and the wing length and width in adults were measured under low power at 120 magnification where 1 unit (one division of the eyepiece micrometer) = 0.015 mm., i.e. 15µ. All other measurements, appearing mostly as ratios in the tables, were made under high power (x 480 magnification) where 1 unit = 0.00345 mm., i.e. 3.45µ. All measurements of larval, pupal and adult characters were made on relaxed specimens cleared in lactophenol.

In the diagnosis of the larval phase only the fourth instar is used since larval characters based on this instar exhibit without significant change, but in slightly larger form, all key characters found in earlier instars. New terminologies are erected for the measurements of key taxonomic characters in these immature stages. Explanations and illustrations of these as well as of adults are given as follows:

A. LARVA

1. Whole larva

(a) Body length (L): Measured from cephalic end of head capsule to end of last abdominal segment in relaxed state of specimen.

(b) Body width (W) to Depth (D) (W/D): The greatest width and depth are measured from the dorsal or ventral view and the lateral view respectively.

2. Head (Fig. 1A, 1B)

(a) HR (Head Ratio, i.e. length (L) / depth (D): The length is measured from the dorsal occipital articulation with the neck to the tip of the mouth from a lateral view, and the depth is measured from the ventral occipital articulation with the neck to the dorsal surface of the head so that the line joining these points is perpendicular to the line describing the length.

(b) OH/v: The length of the head articulation with the neck from the dorsal to the ventral points over the length from the latter point to the tip of the subgenal band of the mouthparts.

(c) qt/ts/sq: 'qt' is the length between the bases of 'q' and 't' setae, 'ts' that between the bases of 't' and 's' setae and 'sq' that between 's' and 'q' setae, all measured from the centre of one base to the other.

(d) L/W: The length (L) seen from the ventral view is measured from the anterior extremity to the posterior while the width (W) is measured from one lateral edge to the other.

(e) tt/ant: This ratio represents the length between the centre of the bases of the 't' setae over that between the centre of the bases of the antennae.

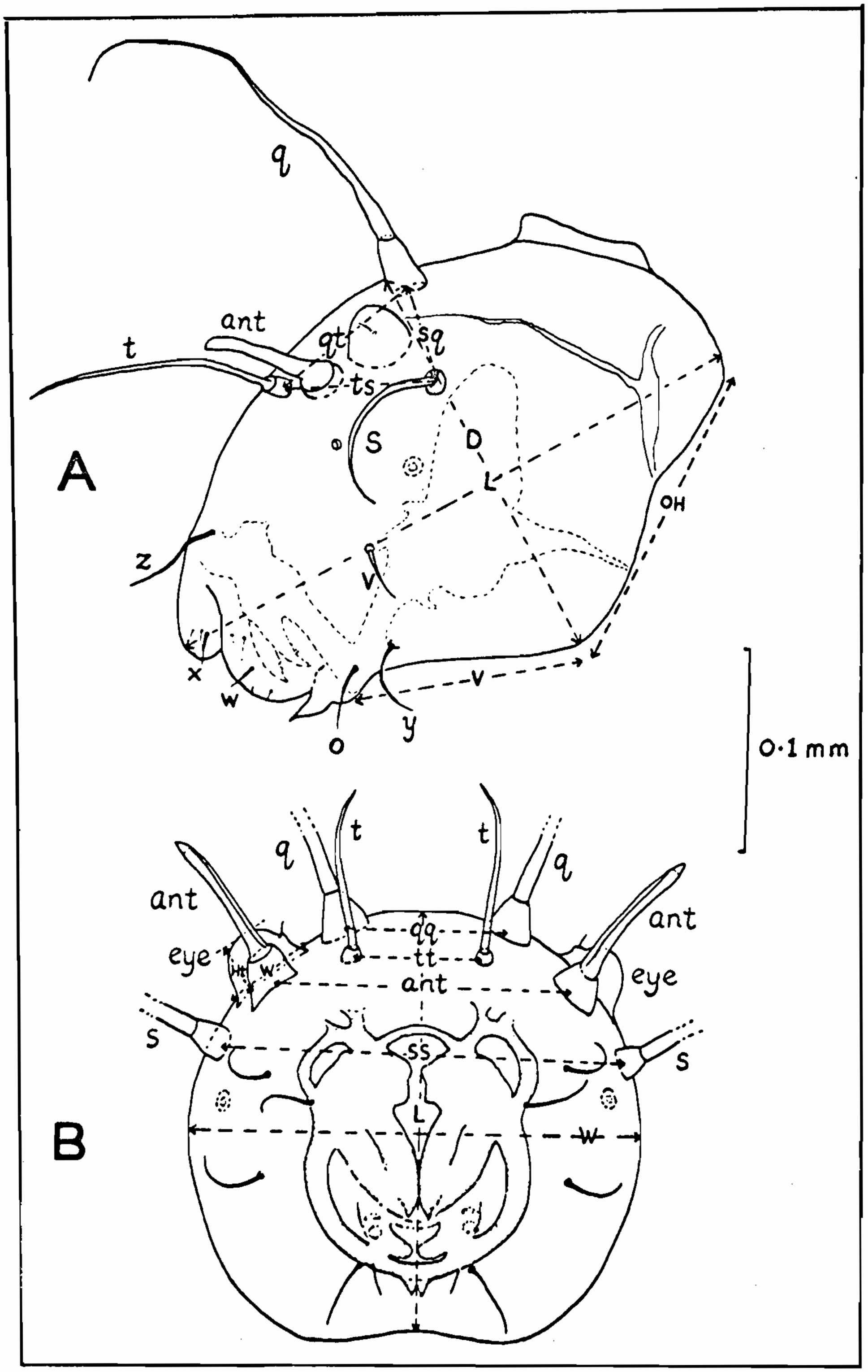
(f) qq/eyes: As in (e) for 'q' setae and eyes.

(g) qq/ss: As in (e) for 'q' and 's' setae.

Fig. 1. Terminologies erected for the measurement of key characters in the larval head, using the fourth-instar larva of *Neoforcipomyia saundersi* n. sp. as example:

A, Lateral view
B, Ventral view

Fig. 1


A
q
ant
t
qt
sq
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S
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V
OH
x
w
o
y
v
0·1 mm
B
q
t
t
q
ant
ant
eye
eye
qq
tt
ant
w
s
s
ss
L
W

(h) AR (Antennal Ratio, i.e. length (L) / width (W)): The antennal length is measured from the base of the antennal filament (tip of tubercle) to its tip and its width at the base.

(i) 'q' and 's' setae: The lengths of the tubercles and filaments are measured, respectively, from the base of the tubercle to the base of the filament and from the base of the filament to its tip. These measurements are not made for all species. In the case of the filaments which are somewhat curved, measurements are made in sections and then added.

(j) Eye (Ht/W): Height (Ht.) of the eye is measured from the base to the apex of the dome (cornea) while the width (W) is the greatest width at the base.

The above measurements (a) to (c) are made from the lateral view; from (d) to (j) from the ventral view.

3. Thorax

(a) Ant. pseud. (Anterior pseudopod): The length (L) and depth (D) are measured from the lateral view while the width (W) is measured from the ventral view.

(b) Proth. setae (Prothoracic setae): Both 'a' and 'b' setae are measured from the lateral view, the length of the tubercle is measured from its base to the base of the setae; the length of the filament is obtained by measuring it in sections from its base to its tip (when it is curved).

Due to the great variation in larval characters, it is not always possible to follow all the above terminologies strictly. This is especially so in species where certain of the setae are absent while in others the relative lengths of the bases of tubercles and filaments do not give a ratio of practical value. In such cases other setae and ratios are used and included in the descriptions.

B. PUPA

1. Whole pupa (Fig. 2A)

(a) Body length (L): Measured from the anterior end (not including tubercles) to the extremity of the last abdominal segment (including processes).

(b) Body width (W): The width is the greatest width in the cephalothorax.

(c) Cephalothorax / Abdomen (Cph/Abd): The cephalothorax is measured ventrally from its anterior end to its ventral tip located generally near the end of the second abdominal segment; the length of the abdomen is measured from the anterior end of the first abdominal segment to the extremity of the last segment (including sexual and terminal processes).

(d) Cephalothorax (Fig. 2A)

2. Cephalothorax

(a) Head/Thorax (Hd/Th): This is the ratio of the head length to the thorax length as illustrated in Fig. 2A.

(b) Respiratory horn: Best illustrated in Fig. 2B.

3. Abdomen

(a) Terminal processes and sexual processes: The lengths and widths of the terminal and sexual processes are illustrated in Figs. 2C, 2D.

Fig. 2. Terminologies erected for the measurement of key characters in the pupa, using _Neoforcipomyia_ _saundersi_ n. sp. as example

A, Female pupa, lateral view

B, Prothoracic horn

HL = Length of respiratory horn
HW = Width of respiratory horn
TrL = Tracheal length
TrW = Tracheal width

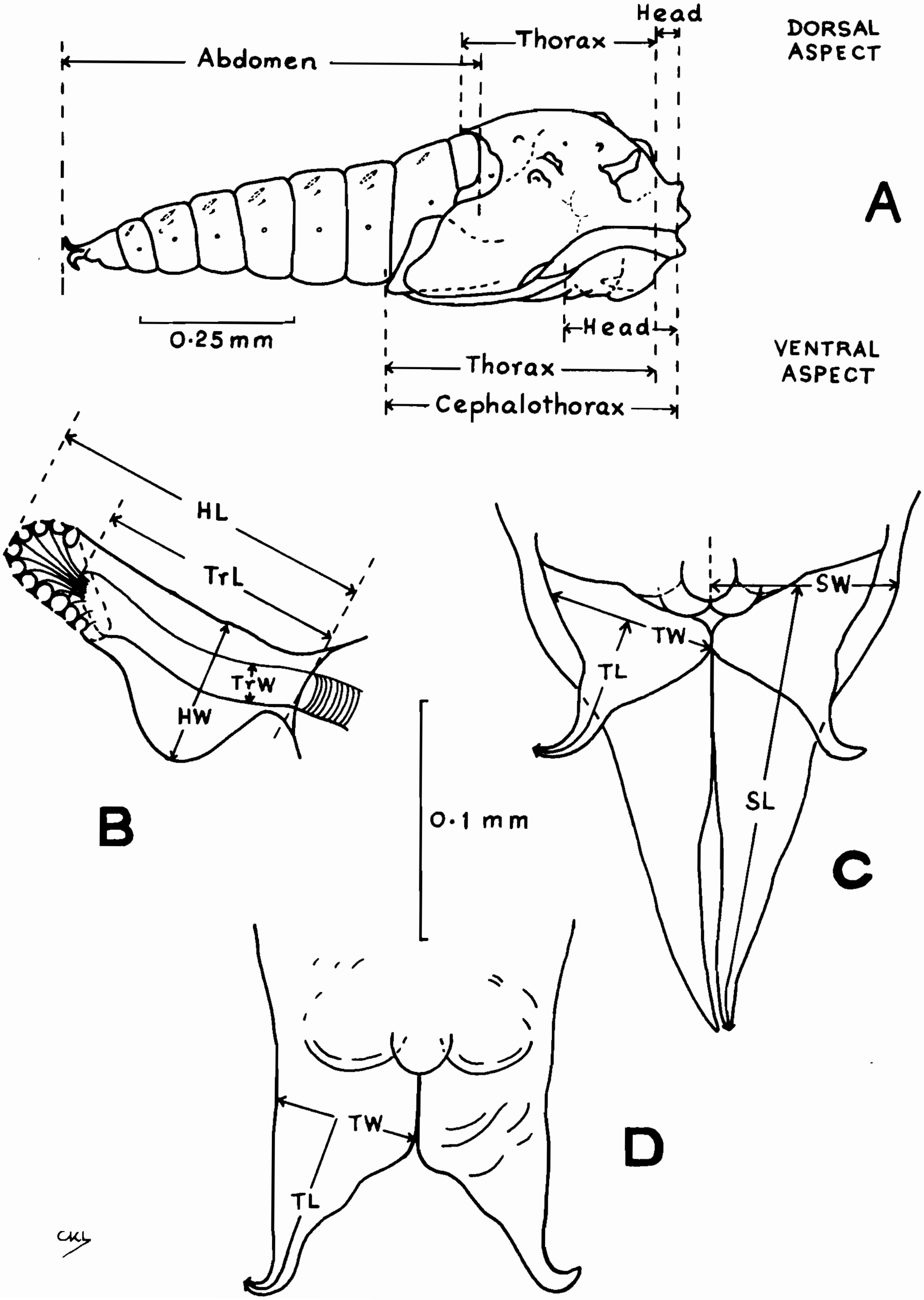
C, Terminal and sexual processes of male pupa

SL = Length of sexual process
SW = Width of sexual process
TL = Length of terminal process
TW = Width of terminal process

D, Terminal processes of female pupa

Abbreviations as in "C"

Fig. 2


Head
Thorax
Abdomen
DORSAL ASPECT
A
0·25mm
Head
Thorax
Cephalothorax
VENTRAL ASPECT
HL
TrL
TrW
HW
B
0·1 mm
SW
TW
TL
SL
C
TW
TL
D
CKL

(b) Third and Last abdominal segments: The length (L), width (W) and depth (D) of the third and last segments as tabulated in Tables 14-31 are self explanatory.

C. ADULT

1. Head

(a) Proboscis/Head (Prob/Hd): The length of the proboscis is measured from the lateral view for both male and female. The head length is also measured from the lateral view, from the base of the proboscis to the vertex of the head.

(b) Antenna: AR is the antennal ratio showing the combined length of the distal five segments (10-14) to that of the basal preceding eight (2-9) taken together in the female (Fig. 3A) and segments 11-14 to segments 2-10 respectively in the male.

2. Thorax

(a) Legs: TR is the tarsal ratio obtained by dividing the length (L) of the basitarsus by that (L_2) of the second tarsomere (Fig. 3B).

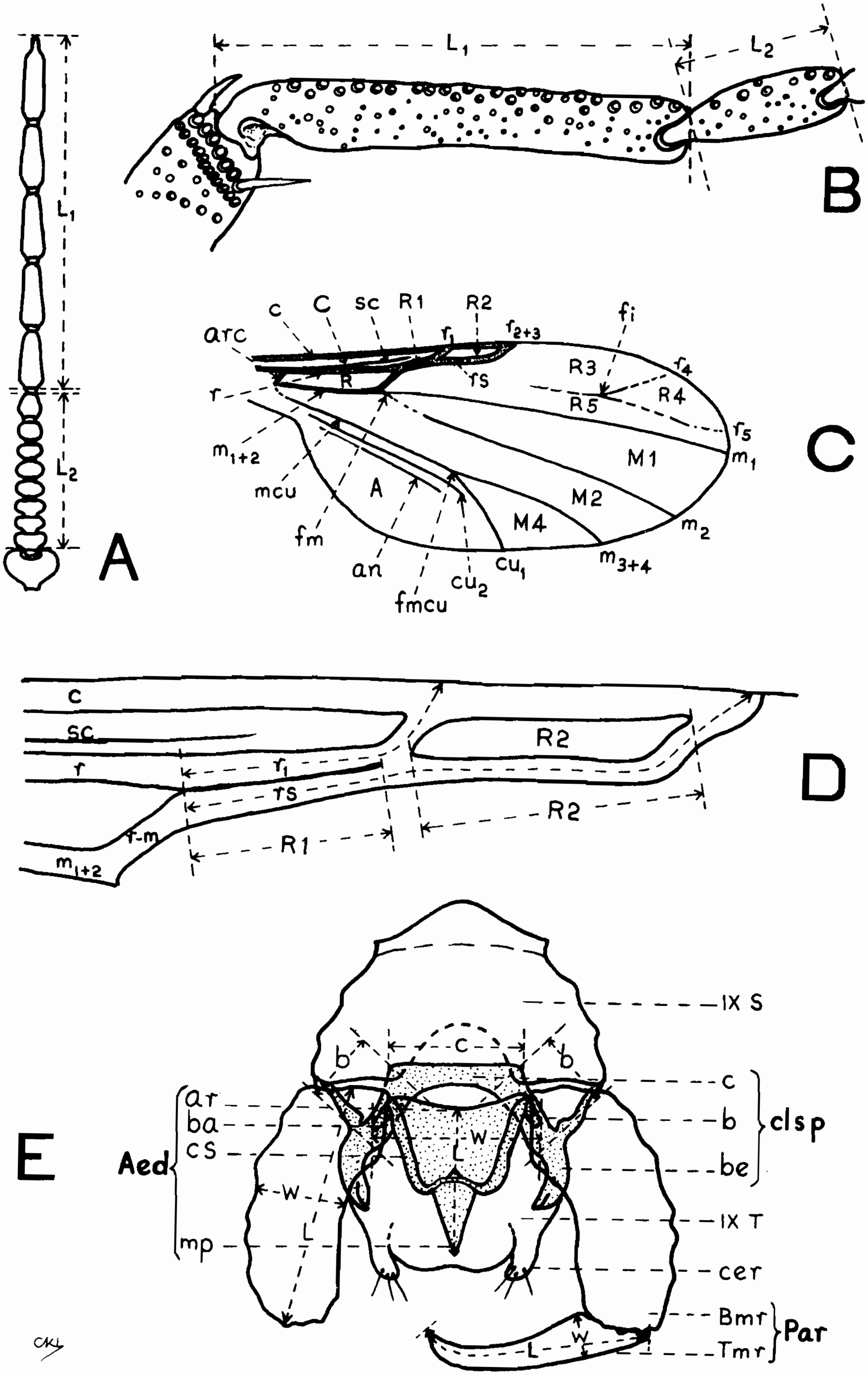
(b) Wing: Wing venation is based on the system of Tillyard (1926), Lee (1947), Wirth (1952) and Tokunaga (1937, 1959, 1962). Wing veins are denoted by small letters while the cells are denoted by capital letters (Fig. 3C). All measurements are done along the veins, directly in some (straight veins) and in sections, which are added, in others (curved veins). Wing length (L) is measured from the basal arculus to the wing tip and the width (W) represents the greatest width. The costal ratio (CR) is the length of the costa (measured from the basal

Fig. 3. Some important terminologies employed in the measurement of key characters in the adult female and male, using *Neoforcipomyia saundersi* n. sp. as example

- A, Female antenna
- B, Female hind leg showing two basal tarsomeres
- C, Female wing:
  - A, anal cell
  - an, anal vein
  - arc, arculus
  - C, costal cell
  - c, costa
  - cu_1, cubitus 1
  - cu_2, cubitus 2
  - fi, intercalary fork
  - fm, median fork
  - fmcu, medio-cubital fork
  - M1, cell M1
  - M2, cell M2
  - M4, cell M4
  - m_1, media 1
  - m_2, media 2
  - m_{1+2}, media 1 and 2
  - mcu, medio-cubital vein or stem of medio-cubital fork
  - R, basal radial cell
  - R1, first radial cell
  - R2, second radial cell
  - R3, cell R3
  - R4, cell R4
  - R5, cell R5
  - r, radius
  - r_1, radius 1
  - r_{2+3}, radius 2 and 3
  - r_4, radius 4
  - r_5, radius 5
  - rs, radial sector vein
  - sc, subcosta
- D, Female anterior wing venation
  - r-m, radio-median cross vein
  - Other abbreviations as in "C"
- E, Male genitalia (hypopygium):
  - Aed, aedeagus:
    - ar, basal arm of aedeagus
    - ba, basal arch of aedeagus
    - cs, caudo-lateral shoulder of aedeagus
    - mp, mesal point of aedeagus
  - clsp, claspettes:
    - b, basal arm of claspette
    - be, posterior extension of basal arm of claspette
    - c, basal union of claspettes

  - Par, paramere:
    - Bmr, basimere
    - Tmr, telomere
  - cer, cercus
  - IXS, 9th sternite
  - IXT, 9th tergite

Fig. 3


L1
L2
A
L1
L2
B
c
C
sc
R1
R2
fi
arc
r1
r2+3
R
rs
R3
r4
r
R5
R4
r5
m1+2
M1
m1
C
mcu
A
M2
fm
M4
m2
an
cu1
m3+4
fmcu
cu2
c
sc
R2
r
r1
rs
R2
D
r-m
R1
m1+2
IX S
b
c
b
c
ar
b
clsp
ba
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Aed
cs
W
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mp
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Par
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Tmr

arculus to the extreme tip of the costa) to the wing length. vLR is the relative length of veins r, m_{1+2} and mcu. RR is the radial ratio showing the relative length of the second radial cell (R2) to the first radial cell (R1) (Fig. 3D). rs/r_1 is the ratio of the lengths of vein rs to vein r_1 and m_{3+4}/cu_1 that of vein m_{3+4} to vein cu_1.

3. Abdomen

(a) Male genitalia: Attention is here drawn to the incorrect usage of some terminologies for certain structures of the male genitalia. Students of the Ceratopogonid male genitalia, "without checking on their credentials" (Snodgrass, 1957, DuPorte, 1965) have been using erroneous terminologies for the varied and complex structure. Snodgrass (loc. cit.) has shown in these insects the two-segmented claspers (variously called "coxites and their styles", "forcep-like genital appendages", "gonopods of the ninth segment") are in actual fact the parameres which closely resemble those of Trichoptera and Mecoptera. The basal segment of these claspers have been called "side-piece", "basistyle" and the distal segment the "clasper" or "distityle". In actual fact they are respectively the "basimere" and "telomere" of the parameres.

What have been called the "parameres" (gonopophyses, harpes, inner processes) in these insects are really the "claspettes" or "claspette lobes" (Snodgrass, loc. cit.). In his descriptions of *Proforcipomyia* species, Saunders (1956) has introduced the term "basistylar apodemes" for the "inner arch" to distinguish them from the "rudimentary parameres". He has defined "parameres" as "slender structures extending backwards above the aegeagus, performing some function at copulation, e.g., in *Forcipomyia* (*Forcipomyia*)" (pers. com.). Most authors have used the terms "parameres" and "basistylar apodemes" synonymously. In fact Saunders in his paper with Ewen (Ewen and Saunders, 1958) and in his later paper (Saunders, 1964) has equated the two terms but in his 1959 paper, in his paper with Chan (Chan and Saunders, 1965) and in his personal communication with Chan, he states that he would now describe the "inner arch" in the Forcipomyia subgenera Lasiohelea, Neoforcipomyia, Dacnoforcipomyia and other forms as "basistylar apodemes" and append "parameres absent" for these forms. Confusion over the precise terminology of the apparently single, composite structure, (i.e. "basistylar apodemes" and their backwardly extending processes or "parameres") is thus evident. This confusion should no longer exist if we resort to Snodgrass' 1957 paper for clarification. As Snodgrass has shown, the claspettes may take on various forms and become greatly modified. His figures of the Forcipomyia (Forcipomyia) claspettes (Snodgrass, 1957, Figs. 13F, 13G) show that the basal arms (b,b) and the basal union (c) of the claspettes correspond to the "basistylar apodemes" of Saunders and the claspette processes (clasp) to the "parameres" of Saunders in Forcipomyia (Forcipomyia) species. Thus, in the above Forcipomyia subgenera where the "inner arch" alone is present, the claspettes are represented by the basal arms and the basal union of the claspettes, the claspette processes being absent. In Neoforcipomyia, however, the basal arms of the claspettes in most species are extended backwards to form the spoon-shaped caudal lobes (Fig. 3E, "b") as in Trichohelea.

The long-established, incorrect usage for the parameres and claspettes should therefore now be rectified.

IV. THE SUBFAMILY FORCIPOMYIINAE LENZ (1934)

The monophyletic subfamily Forcipomyiinae has been variously divided and classified as follows:

"Genuine Group" Kieffer (1925), Faune de France 11: 1-139

Forcipomyinae Lenz (1934), in Lindner's Der Fleigen der Pal. Reg. 13a:97

Forcipomyiinae Enderlein (1936), Tierwelt Mitteleur 6: 50;
Wirth (1952), Univ. Calif. Publs. Entomol. 9: 116

Atrichopogon and Forcipomyia Groups of Mayer (1934), Macfie (1940),
Johannsen (1943), Lee (1947) and others mentioned
in the text.

Diagnosis (original).-

Larvae terrestrial or aquatic, with both prothoracic and anal pseudopods (prolegs), bearing one or more rows of hooklets; all body segments with short or long spines. Head typically hypognathous but may be prognathous (Warmkea, Trichohelea) or semi-hypognathous (Proforcipomyia); mouthparts well developed, pharyngeal skeleton with about six combs, angulus with bristles.

Pupae typically retaining last larval exuviae, body segments bearing tubercles or stump-like projections or branched projections on first five abdominal segments (most Atrichopogon) or on all but last segment. Prothoracic respiratory horns (trumpets) typically short and knob-like.

Adults rather short and stout bodied, slightly hairy (Atrichopogon) or very hairy (others). Eyes pubescent or bare. Antennae typically 14-segmented but 10-segmented in some females of Trichohelea; last five to seven flagellar segments in females and last four in males usually elongate with last segment usually ending in a nipple. Maxillary palps typically 5-segmented, rarely 4-segmented, with last two segments fused;

third segment typically largest and bearing sensilla scattered over its surface or concentrated in a sensorium. Legs with well-developed or very large empodium except Trichohelea males where it is vestigial or absent; claws present or absent (some Pterobosca). Wings with microtrichia well-developed (Atrichopogon) or minute (others); macrotrichia sparse, suberect, fine and confined to wing tip or absent (Atrichopogon), or dense, depressed, elongate, sometimes scale-like (others); costa reaching just short of or to middle or beyond or to two-thirds of wing, with second radial cell open or almost obliterated and longer or shorter than first which is usually narrow and almost obliterated. One or two spermathecae. Male hypopygium with claspettes absent or small and hook-shaped (Atrichopogon) or variously modified (others); aedeagus more or less shield-shaped or bipartite or complicated with outward-turning hooks.

V. RECLASSIFICATION OF THE FORCIPOMYIINAE

The fluidity and lack of objective methods of assigning different taxa to their appropriate position in the hierarchy in insects (as well as in other animals) are weaknesses in systematics (Blackwelder, 1959; Kevan, 1961). Most specialists tend to elevate their groups, without reference to other groups, to higher and higher levels in the hierarchy, or in some cases, fail to give their groups the appropriate level in the hierarchy. Since opinions often differ, even among specialists, on the proper recognition of a particular group at one level in the hierarchy or another it is of relatively little importance in the initial classification of a group not sufficiently well known, whether it is placed at one level in the hierarchy or another, so long as it is reasonably homogeneous. According to Curran (1934) and Kevan (1965, pers.com.) for example, subgenera "are superfluous" (Curran, loc.cit.) and are often "proposed as a rule because the author hopes that some day some character may be found upon which a distinct genus may be based." The latter emphasizes that it is of importance that the group in question should be "approximately equated with comparable related groups" (Kevan, 1961). An objective approach to the problem of status is therefore needed.

In the Ceratopogonidae, the large polytypic genus Culicoides has received more attention than any other group and, as a result, its systematic position and classification are relatively better developed than for other genera in the family. Characters in all stages in this genus are remarkably homogeneous and the division of the genus into subgenera is difficult. Foote and Pratt (1954) has remarked that "it is nearly impossible to divide the genus Culicoides ... into well-marked subgenera on the basis of more than a single character; therefore the authors have made no attempt to erect subgenera." Khalaf (1954), Fox (1955), Vargas (1960) and Wirth and Hubert (1959) have however attempted to divide the genus into a number of subgenera but all these authors have likewise shown the lack of distinct good subgeneric characters.

In the immature stages, for example, variation in morphological characters, especially in larvae, is so small that even differentiation on the specific level is often difficult, and no one has as yet succeeded to divide the genus into subgenera on basis of the early stages although the genus is better known than *Forcipomyia*. Similarly, in the adult, *Culicoides* males have such homogeneous genitalic structures that division of the genus into subgenera on these structures alone is unreliable. In the female, variation in color patterns appears to be great and fairly distinct but this is only of specific value.

In contrast to *Culicoides*, the genus *Forcipomyia* has been shown by Saunders (1956, 1959, 1964) to be very variable in both immature and adult characters so that its division into a number of subgenera is readily ascertained. Each subgenus in the genus is distinct and readily separated from every other subgenus and is completely homogeneous within itself. On the basis of immature stages alone, no difficulty has been experienced in separating the subgenera except in the pupae of *Lasiohelea* s. str., *Dacnoforcipomyia*, *Thyridomyia* and *Synthyridomyia* and in some larvae of *Thyridomyia* and *Lasiohelea* s. str. In the adult, male genitalia are so distinct in each subgenus, except *Forcipomyia* s. str. and *Warmkea*, that division of the genus into subgenera on genitalic characters alone was entirely justifiable. Adult females of the subgenera, however, can be separated only by combinations of characters. Nevertheless, comparisons in all stages between the two large polytypic genera, Culicoides and Forcipomyia, show clearly that the critera used for subgeneric assignment in the two genera are widely different. For Forcipomyia subgenera, the criteria used being more reliable are unquestionably far higher than, and not equivalent to, those used for Culicoides subgenera so that when the former group (Forcipomyia) is equated to the latter (Culicoides), particularly with reference to male genitalia, Forcipomyia subgenera warrant generic status. In other words, Forcipomyia genera are based on morphological characters that have such a high degree of reliability that they warrant generic status (Curran, 1934; Kevan, 1965, pers.com.).

A further consideration in support of the elevation of Forcipomyia subgenera to generic status is the evidence from the other genus of the subfamily Forcipomyiinae, namely Atrichopogon. As shown by Ewen and Saunders (1958) there is no single character in the immature stages of Atrichopogon that can separate these stages from those of Forcipomyia. Also differences between the immature stages in the Forcipomyia, as for example between Trichohelea and Forcipomyia s. str. or Neoforcipomyia and Thyridomyia, are far greater than those between some Forcipomyia species and some Atrichopogon species. On characters of immature stages therefore, e.g. between Forcipomyia s. str. spp. and Atrichopogon crinitus or between Thyridomyia spp. and Atrichopogon fuscus, Atrichopogon may well be classified as a subgenus of Forcipomyia. Ewen and Saunders (1958) pointed out that "most Atrichopogon larvae are unmistakable in their flattened spiny state." This is a good generalization on the whole but some species are practically cylindrical and others squarish in cross section. In the genus Forcipomyia some Thyridomyia species also have the flattened spiny condition so that in reality there is no single character in the immature stages (including the pupa as shown by Ewen and Saunders) which can separate the two genera.

It may of course be argued that the two genera are distinct in the venation and chaetotaxy of the adult wing. These distinctions could however be due to evolutionary divergence (adaptive radiation) of the same phenotype and besides, they are actually not as great as generally believed. The elongated second radial cell due to extension of the costa to two-thirds the length of the wing in Atrichopogon is also found in Forcipomyia (Lasiohelea), and Forcipomyia (Dacnoforcipomyia), and Warmkea species, although the cell in Lasiohelea and Dacnoforcipomyia species is distinctly narrower. The chaetotaxy of the wing in Forcipomyia is different from that of Atrichopogon in the generally denser and thicker and more decumbent macrotrichia and more minute microtrichia but within the genus these features vary somewhat from group to group, especially in Lasiohelea where they are intermediate between Forcipomyia s. str. and Atrichopogon (Kieffer, 1921; Edwards, 1922; Lee, 1954). The possibility exists that forms with characters intermediate between Atrichopogon and Lasiohelea might be discovered. In any case, the distinction between the two genera based solely on wing characters should be subordinate to that based on a sum total of characters of all stages. A full discussion of the status of Atrichopogon is given in Section V from which it will be clear that the genus has only equivalent status to most subgenera of Forcipomyia. But since Atrichopogon has always been recognized as a distinct genus in the subfamily, and the writer agrees that this has been appropriate, the status of Forcipomyia subgenera should be re-evaluated, i.e. raised. It does not merit a generic status according to Saunders' (1956) criteria for Forcipomyia subgenera.

Another point in favour of raising the status of Forcipomyia subgenera to the generic level (for some of them, not all) is that the temporary artificial classification of the "Lasiohelea complex" of Saunders (1964) could be approached more objectively. Saunders (1964) has coined the term "Lasiohelea complex" to include Forcipomyia subgenera having in common "an elongated second radial cell in the wing." This complex would now include the following subgenera: Lasiohelea, Neoforcipomyia, Warmkea, Dacnoforcipomyia, "New subgenus" (Lane's (1947) Lasiohelea stylifer Lutz) if correctly identified, Caloforcipomyia, and perhaps some Trichohelea species and some Thyridomyia species like esakii Tokunaga, hamata Tokunaga etc. as well. If Pterobosca Macfie were to be included as a subgenus of Forcipomyia, as proposed by Tokunga and Murachi (1959) and if Harant and Huttel's (1951) genus Parapterobosca were to be included as a subgenus of Forcipomyia, these two "subgenera" should also be included in the "Lasiohelea complex". Since the characters of immature stages and of the adults differ considerably in all these subgenera, except in Lasiohelea, Dacnoforcipomyia, Lane's Lasiohelea stylifer Lutz and Thyridomyia, this classification is artificial and serves at best to pool unknowns for which a natural classification can eventually be determined. Similarity in the elongated second radial cell in these apparently unrelated subgenera is indicative here not of really close affinity but of convergence resulting from adaptation to a similar mode of life, probably that of effective flight associated with biting habit which is particularly pronounced in Lasiohelea, Dacnoforcipomyia and Neoforcipomyia but not yet known in other subgenera.

In the case of Lasiohelea and Dacnoforcipomyia Lane's Lasiohelea stylifer Lutz and Thyridomyia, however, the many similar characters shared by them in immature as well as adult stages do show close affinity because this conclusion is based on a sound principle of all taxonomy with regard to conclusions on affinities (based largely on homologies, not homoplasies) i.e. the greater the number of similar characters involved between two groups, the stronger is the affinity. Their extreme close affinity, as has been made clear in Saunders' (1956) revision of *Forcipomyia* and in Chan and Saunders' (1965) paper on *Dacnoforcipomyia anabaenae*, denies them as a group together with the similarly closely related *Synthyridomyia* and Lane's *Lasiohelea stylifer* Lutz, the status given to most of the other *Forcipomyia* "subgenera". The status of the various groups in the "*Lasiohelea* complex" can thus be brought out and approximately equated.

A final point in support of the change in taxonomic status of the *Forcipomyia* subgenera (some, not all) is the consistent uniformity of subgeneric characters that can be dependably relied upon in separating the groups distinctively. The characters that have been found most reliable are those of the immature stages and male genitalia as shown by Saunders (1956). Characters of immature stages are reliable because immature stages of phylogenetically related forms are commonly more similar than those of the adults, a fact noted by von Baer even before the phylogenetic implications were known. The opposite can nevertheless occur (Simpson, 1961). *Warmkea* is considered such a case, the subgenus being considered as having secondarily adapted to a semi-aquatic sort of life in the leaf axils of water-holding plants - hence the divergence of immature forms from the basic *Forcipomyia* s. str. phenotype. Those of the male genitalia are also reliable because genitalic structures are generally considered to be good indicators of common ancestry due to their nonadaptive nature (and hence less labile) in response to varying ecology. This, however, is only a broad generalization since truly nonadaptive characters seem to be extremely rare and are seldom if ever certainly identifiable as such (Simpson, 1961). Female characters have not been found reliable at the subgeneric level. They have been found to overlap. Combinations of characters however can be used for subgeneric separation but they are not practical in normal taxonomic work.

Since adult *Atrichopogon* and *Forcipomyia* females as a whole are remarkably uniform even between species aside from some quantitative variation, the prevailing phenotype must obviously be the female. This morphological monotony of Forcipomyiinae female adults with their great proliferation of species somewhat parallels that of *Drosophila* (Dobzhansky, 1961) and like the latter genus, seems to be an indication of a high degree of perfection of external morphology due to environmental adaptation. Lerner (1954) has pointed out that natural selection acts on populations to maintain optimal phenotype and discriminates any phenodeviants. Mayr (1963) has similarly pointed out that phenotypic stability is a means whereby genetic variation is protected ecologically against elimination by selection. Since selection acts on phenotypes, and since phenotypes are produced by genes that are intimately welded together into a single closely knit whole through pleiotropy, dominance (and overdominance), epistasis, and polygeny (Mayr, 1963), any selection for a new phenotype will force the abandonment of the previously integrated genotype and will thus lead to lowered fitness, due to either an accumulation of homozygous recessives or a disharmony between the newly favoured genes and the remainder of the genotype. In *Atrichopogon* and *Forcipomyia* it is clear that phenotypic stability or lack of phenodeviants shows that stabilizing (normalizing plus canalizing) selection (Waddington, 1957, 1960) due to genetic homeostasis is strong. The Forcipomyiinae as a group is therefore evolutionary successful in terms of fitness.

From comparative morphology, with particular reference to male genitalia in '<u>Forcipomyia</u>', and from the criteria used in their separation with reference to those used in the better studied and comparable genus <u>Culicoides</u> as well as from considerations of <u>Atrichopogon</u> characters, the following classification of the subfamily Forcipomyiinae, is proposed.

<u>Proposed Classification of the Subfamily Forcipomyiinae</u>

- Genus <u>Proforcipomyia</u> Saunders (1956)
- Genus <u>Caloforcipomyia</u> Saunders (1956)
- Genus <u>Metaforcipomyia</u> Saunders (1956)
- Genus <u>Forcipomyia</u> Meigen
    - Subgenus <u>Forcipomyia</u> Meigen (1818)
    - Subgenus <u>Warmkea</u> Saunders (1956)
    - Subgenus <u>Schizoforcipomyia</u> Chan (1965), new subgenus
- Genus <u>Atrichopogon</u> Kieffer
    - Subgenus <u>Atrichopogon</u> Kieffer (1906)
    - Subgenus <u>Meloehelea</u> Wirth (1956)
- Genus <u>Lasiohelea</u> Kieffer
    - Subgenus <u>Lasiohelea</u> Kieffer (1921)
    - Subgenus <u>Dacnoforcipomyia</u> Chan and Saunders (1965)
    - New Subgenus (Lane's <u>Lasiohelea stylifer</u> Lutz)
    - Subgenus <u>Thyridomyia</u> Saunders (1956)
    - Subgenus <u>Synthyridomyia</u> Saunders (1956)
- Genus <u>Neoforcipomyia</u> Tokunaga (1959)
- Genus <u>Trichohelea</u> Goetghebuer (1920)
- Genus <u>Pterobosca</u> Macfie (1932)
- Genus <u>Parapterobosca</u> Harant and Huttel (1951)

Tokunaga and Murachi's (1959) subgenera "A", "B", "C" and "D" require confirmation from immature stages as do the genera Parapterobosca and Pterobosca.

The above proposed classification of the subfamily Forcipomyiinae may prove generally acceptable but more knowledge especially of the early stages representing a wide range of species, is necessary for a more critical evaluation of the present treatment.

A key for the determination of genera and subgenera represented in the proposed classification follows. All known species in these categories are not included as the identification of many species is still in an unsatisfactory state.

VI. DIAGNOSIS OF AND KEYS TO GENERA AND SUBGENERA OF FORCIPOMYIINAE TOGETHER WITH DESCRIPTION OF NEW SPECIES

A(i). KEY TO GENERA OF FORCIPOMYIINAE (LARVA)

1\. Head prognathous, dorso-ventrally flattened............ *Trichohelea*

Head prognathous, semihypognathous or hypognathous, never dorso-ventrally flattened............................ 2

2(1). Head semihypognathous, profile scalloped, with two slight hollows or flat regions, antennal filament long; cauda long, pointed, fringed with setae.................................. *Proforcipomyia*

Head prognathous or hypognathous, profile smoothly rounded, antennal filament long or short; cauda short or absent or moderately long but without fringe of setae.............................. 3

3(2). Head and body with knob-like chaetae bearing tubes and cones of wax........................... *Metaforcipomyia*

Head and body without knob-like chaetae bearing tubes and cones of wax.................................. 4

4(3). Last abdominal segment bearing large dorsal chitinous process with two basal and two long terminal stout setae................................ *Caloforcipomyia*

Last abdominal segment without large dorsal chitinous process;.. 5

5(4). Body with two pairs prothoracic large, hook-tipped setae and one similar or modified pair on penultimate segment, and with complex, rosette-like lateral setae.................... *Neoforcipomyia*

Body with setae not arranged as above........................... 6

6(5). *a* setae spear-shaped................................ *Forcipomyia*

a setae not spear-shaped... 7

7(6). Prothoracic pseudopod always divided; body usually flattened with lateral processes at least as long as segments; antennae usually with filaments borne on long tubercles; head with four pairs of pits............................ *Atrichopogon*

Prothoracic pseudopod usually undivided, rarely divided; body usually cylind~~t~~rical, rarely flattened; lateral processes rarely as long as segments; antennae usually with filaments borne on short tubercles or with very reduced filaments; head with two pairs of pits.......... *Lasiohelea*

A(ii). KEY TO GENERA OF FORCIPOMYIINAE (PUPA)

1. Posterior median point of mesothorax not overlapping first abdominal segment.................................... 2

Posterior median point of mesothorax overlapping first abdominal segment.................................... 3

2(1). Terminal processes of last abdominal segment with seta on outer surface................................Trichohelea

Terminal processes of last abdominal segment without seta on outer surface................................Atrichopogon

3(1). Male sexual processes ventral.................................... 4

Male sexual processes dorsal.................................... 5

4(3). Rupa yellow: Male sexual processes rather long, closely appressed; posterior median point of mesothorax at or just overlapping anterior border of first abdominal segment................................Neoforcipomyia

Rupa orange: Male sexual processes relatively shorter or very short; posterior median point of mesothorax overlapping first abdominal segment more or less to middle of segment or beyond, rarely just overlapping................................Lasiohelea

5(3). Terminal processes long; usually with a prominent pair of setigerous processes on thorax just above and behind prothoracic horns.................................... 6

Terminal processes short or relatively shorter; rarely with a prominent pair of setigerous processes on thorax just above and behind prothoracic horns..................... 7

6(5). Prothoracic horn usually expanded apically, always bearing a double palisade' of spiracular papillae in partial or complete circle........................Proforcipomyia

Prothoracic horn slender, not expanded apically, with a row of spiracular papillae across extremity........Caloforcipomyia

7(5). Prothoracic horns slender, with a row of spiracular papillae over apex to halfway down stem............Metaforcipomyia

Prothoracic horns with a row of spiracular papillae over apex only....................................Forcipomyia

The immature stages of the provisional genera Parapterobosca and Pterobosca are as yet unknown.

' Term used by Saunders to mean "leaf-like layer"

A(iii). KEY TO GENERA OF FORCIPOMYIINAE (ADULT MALE)

1. Claspettes lacking or when present simple and hook-shaped.. *Atrichopogon*

Claspettes always present, not simple and hook-shaped................2

2(1). Basal arms of claspettes extended posteriorly into caudal lobes...3

Basal arms of claspettes not extended posteriorly into caudal lobes...4

3(2). Claspettes H-shaped, with horizontal cross bar joining bases of basal arms of claspettes...........*Trichohelea*

Claspettes not H-shaped but a massive arch-like structure...*Neoforcipomyia*

4(2). Claspette processes entirely fused in mid-line, forming a long, lanceolate, median common lobe...*Metaforcipomyia*

Claspette processes not entirely fused or fused at base or entirely separate or absent............................5

5(4). Claspettes without basal union and processes; basal arms united apically forming an inverted V with sharply pointed top.........................*Caloforcipomyia*

Claspettes (i) with basal arms, basal union and with or without processes or (ii) with basal arms and basal union (without processes) or without basal union (with processes) or (iii) with basal arms, without processes and with or without basal union..6

6(5). Claspette processes usually long, filiform and parallel, fused at base or entirely separate or when absent, claspettes arch-like with aedeagus a V, bearing small sclerites at posterior apex...................................*Forcipomyia*

Claspette processes absent or when present, short; processes separate and triangular or club-shaped, or filiform, separate or joined medially...7

7(6). Claspette processes always present, club-shaped, hook-shaped, triangular or filiform...........*Lasiohelea* (part) (Subgenera *Synthyridomyia*, *Thyridomyia*)

Claspette processes absent or vestigial............................8

8(7). Claspettes slender, arch-like or an inverted V with small, round top; aedeagus usually shield-shaped, subtriangular and sometimes consisting of small sclerites; wing with second radial cell short and bare areas along veins absent or indistinct.........................Proforcipomyia

Claspettes slender, arch-like; aedeagus complicated, usually with outward-turning sclerites at apex; wing with second radial cell elongated and narrow and with bare areas along veins distinct......Lasiohelea (part)
(Subgenera Lasiohelea,
Dacnoforcipomyia, Lane's
Lasiohelea stylifer Lutz --
New Subgenus)

A(iv). KEY TO GENERA OF FORCIPOMYIINAE (ADULT FEMALE)

1. Wing without vein m2....................................Metaforcipomyia

Wing always with vein m2..2

2(1). Apical six or seven antennal segments distinctly longer than preceding basal segments..............................3

Fewer than six antennal segments distinctly longer than preceding basal segments.......................................4

3(2). Legs with empodia very broad and scalloped; hind TR 3.0 or greater....................................Pterobosca

Legs with empodia well-developed but not very broad and scalloped; hind TR 2.2.........................Parapterobosca

4(2). Wing with sparse, erect macrotrichia over surface, sometimes absent or only at wing tip; microtrichia well-developed; costa reaching well beyond middle of wing, usually extending to two-thirds of wing; second radial cell elongate and always open...................................Atrichopogon

Wing with dense, decumbent, elongate or often scale-like, macrotrichia; microtrichia minute; costa reaching near middle of wing or beyond, rarely extending to two-thirds of wing; second radial cell short or when elongate, usually practically closed...5

5(4). One spermatheca...6

Two spermathecae...8

6(5). Second radial cell elongate; maxillary palpal segments 4 and 5 incompletely segmented, partly or completely fused.................... Forcipomyia (part)

Second radial cell short or elongate; maxillary palpal segments 4 and 5 completely segmented or completely fused..7

7(6). Maxillary palpal segments 4 and 5 completely segmented.. Lasiohelea

Maxillary palpal segments 4 and 5 completely fused.. Forcipomyia (part)

8(5). Basal flagellar segments slender, elongate, two or even three times as long as wide. (Most, not all, with metallic jade green or deep blue pigmentation).............................. Calof orcipomyia

Basal flagellar segments shorter than twice of width, flask-shape, short-oval, subspherical or more or less flattened and discoidal.........................9

9(8). Costa reaching well beyond middle of wing; TR of hind legs larger than 2.0 in both sexes........................10

Costa reaching near, at or slightly beyond middle of wing; TR of hind legs less than 2.0 in both sexes...11

10(9). Basal flagellar segments of antenna compressed and distinctly discoidal, reduced in number or normal; flagellar segment 10 longer than twice length of 9; scutellum with few bristles............ Trichohelea

Basal flagellar segments of antenna very slightly transverse, but gradually elongate distally, becoming slightly longer than wide at segment 9 and generally subspherical, rarely discoidal; flagellar segment 10 shorter than twice length of 9; scutellum with many bristles............... Neoforcipomyia

11(9). Maxillary palpal segments 4 and 5 broadly joined together, becoming completely fused in some, segment 3 with shallow sensorium or with scattered sensillae without sensorium; wing unadorned, macrotrichia slender, costa usually reaching middle of wing or slightly beyond; legs never marked with colored spots or bands and without broad scales (sometimes with very slender scales); hind TR 0.6-2.0................. Proforcipomyia

Maxillary palpal segments 4 and 5 narrowly joined together, never fused, segment 3 with deeply or distinctly sunken sensorium; wing almost always adorned with light and dark macrotrichia (often broad scales), costa usually reaching before middle of wing; legs usually with colored bands of markings and rather broad scales; hind TR usually 0.5-1.33..............................*Forcipomyia* (part)

B. GENUS *PROFORCIPOMYIA* SAUNDERS (1956)

Type species *wirthi* Saunders (1956)

DIAGNOSIS

The following diagnosis of the immature stages is Saunders' (1956):

"*Larva*.- Head semihypognathous; profile with two slight hollows or flat regions, not smoothly rounded; labrum with nose-like protuberances; mandibles broad apically, with right-angled twist; antennae usually slender, long and backward-curving. Body often with faint reddish pigment pattern in subcutaneous fat body. Prothoracic pseudopod a simple spinose cushion rarely surmounted by a pair of papillae bearing longer hooklets. Anal pseudopod a transverse ridge bearing two rows of hooklets, sometimes large and long. Cauda long, pointed, fringed with setae.

Pupa.- Without large cuticular spine-like processes; rarely retaining larval exuviae. Prothoracic horns variable in size and shape, always bearing a double palisade of spiracular papillae in partial or complete circlet. Male sexual processes dorsal."

Adult female.- Basal eight flagellar segments flask-shaped, distal five elongate. Maxillary palp five-segmented, last two segments rarely incompletely fused; segment 3 usually with small shallow sensorium. Wings and legs unadorned. Wings rather densely haired, with slender macrotrichia, bare areas along veins indistinct; costa reaching middle of wing or slightly more, first radial cell slit-like or absent, second radial cell subtriangular, not very long and rarely absent. TR of hind legs 0.6-2.0. Two spermathecae.

Adult Male.- Antennae with basal nine flagellar segments flask-shaped only four distal segments elongate. Other features as in female, with usual sexual differences. Genitalia with aedeagus subtriangular, shield-shape and rarely serrate on caudal margin or transverse and band-like; claspettes arch-like, rarely with rudimentary processes.

Proforcipomyia clara CHAN NEW SPECIES

Larva.-

Length of full grown fourth instar 2.76 mm. Color (preserved) pale, with reddish brown pigment pattern in dorsal fat body of thorax.

Head light brown, with usual scalloped profile. p hairs lanceolate, q hairs spoon-shaped, all other hairs simple (Fig. 4B). HR 1.56; OH/v 1.75; pq/qt/ps 1.18: 1: 2.18; tt/ant 0.37; qq/eyes 0.4; qq/ss 0.34; pp/ant 0.74.

Chaetotaxy on first ten body segments similar, each segment with the usual pair of lanceolate a hairs, five pairs long, fine lateral hairs and one pair minute hairs (Fig. 4A). Penultimate and last segments each with only three pairs of the long, fine lateral hairs. Prothoracic pseudopod (Fig. 4C) the usual spinulose cushion with length, width and depth in proportion of 2.05: 1.95: 1. Posterior pseudopod (Fig. 4D) a transverse ridge bearing a posterior row of eight long black hooklets and an anterior row of ten smaller hooklets; anal blood gills four, rather small and pointed at tip. Cauda long, tapering, fringed with small setae, slightly longer than last abdominal segment.

Pupa.-

Length 2.01 mm. in female and 1.98 mm. in male.

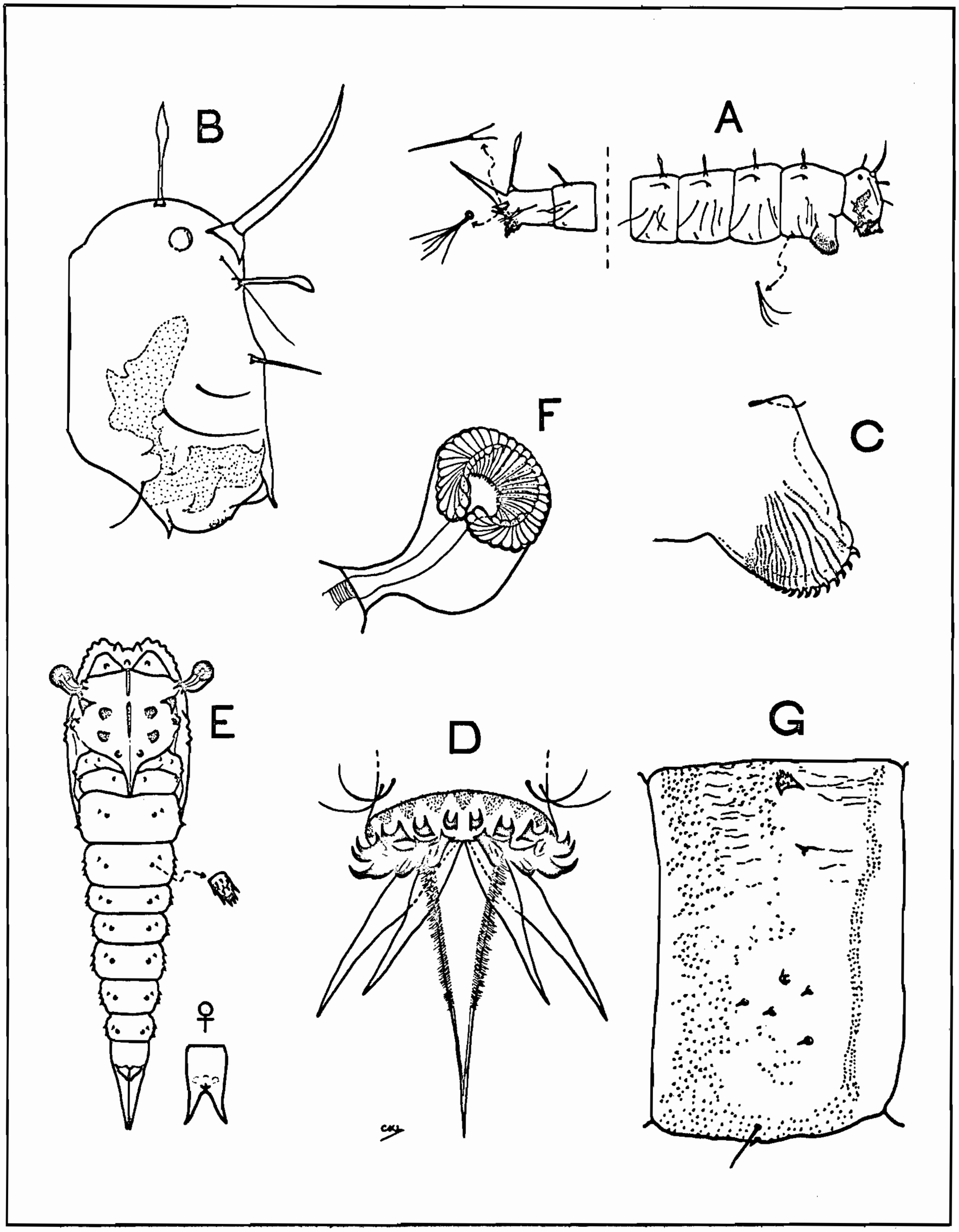
Median head sclerite bearing three tubercles and lateral sclerites each bearing one tubercle. Cephalothorax 1.59 as long as its width in female and 1.81 in male; ratio of length of head to that of thorax 0.46 in ventral aspect and 0.18 in dorsal aspect in female and respectively

Fig. 4. _Proforcipomyia_ _clara_ n. sp.

A-D, Fourth-instar larva:
  - A, Anterior and posterior portions
  - B, Head
  - C, Prothoracic pseudopod
  - D, Anal pseudopod

E-G, Pupa:
  - E, Pupa, dorsal view
  - F, Prothoracic horn
  - G, Third abdominal segment

Fig. 4



0.45 and 0.22 in male.

Thorax bearing on dorsum two median ridges and six pairs of tubercles, the anteriormost pair just in front of prothoracic respiratory horns; largest pair just posterior to horn and setate, the rest non-setulose. Prothoracic horn (Fig. 4F) with typical rounded expansion at apex and bearing 22 spiracular papillae in the upper palisade and 36 in the lower palisade in the female and respectively 11 and 22 in the male; horn length 1.92 times its width in female and 2.39 in male; tracheal length to horn length 0.73 in female and 0.79 in male.

Abdominal segments 3-7 similar in chaetotaxy, each segment bearing two pairs dorsal, two pairs ventral and five pairs lateral tubercles (Fig. 4E, 4G); segments 2 and 8 also each bearing two pairs dorsal tubercles but only three pairs lateral and two pairs ventral tubercles respectively (Fig. 4G). Terminal processes sharply pointed, divergent in female, closely appressed in male, with length, width and depth in proportion of 3.25: 1.67: 1 in female and 4.13: 1.20:1 in male. Male sexual processes dorsal, small, short, with length, width and depth in proportion of 2.5:2.5: 1.

Adult Female.-

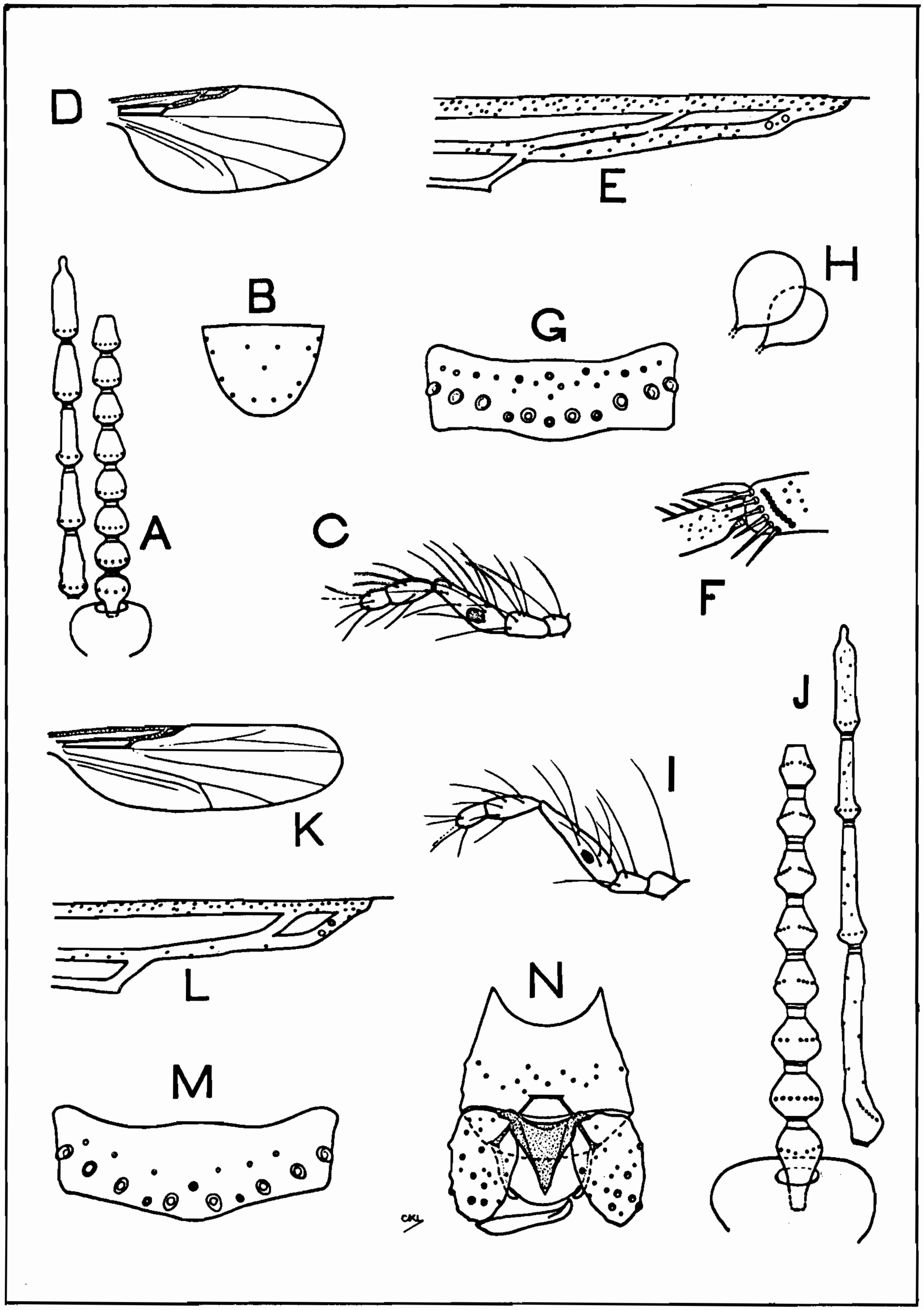
Length 1.32 mm. Wings (Fig. 5D) 0.78 x 0.36 mm.

Head with antennae and mouthparts light brown, eyes and pedicels dark brown; clypeus (Fig. 5B) with 14 bristles; proboscis more than half length of head capsule (0.57: 1); antenna (Fig. 5A) with segment 3 wider than long, segment 4 about as wide as long and segments 5-9 longer than wide; segments 10-14 elongate; AR 1.15. Maxillary palp (Fig. 5C) rather slender with segments in proportion of 5.5: 8: 19: 11: 7; last two segments united broadly at joint; segment 3 long, slightly swollen at base and bearing a deep sensorium with sessile sensilla; PR 2.71.

Fig. 5. Proforcipomyia clara n. sp.

- A-H, Adult female:
  - A, Antenna
  - B, Clypeus
  - C, Maxillary palp
  - D, Wing
  - E, Anterior wing venation
  - F, Hind tibial comb
  - G, Scutellum
  - H, Spermathecae
- I-N, Adult male:
  - I, Maxillary palp
  - J, Antenna
  - K, Wing
  - L, Anterior wing venation
  - M, Scutellum
  - N, Genitalia

Fig. 5



Thorax dark brown; scutellum bearing 11 large bristles in row across posterior margin, other smaller bristles arranged as shown (Fig.5G). Legs uniformly light brown, with TR 1.68 in fore leg, 1.28 in middle leg and 1.17 in hind leg; tibial comb in hind leg bearing seven bristles.

Wings brown, CR 0.43. Venation: vLR 1.11: 1: 2.49; rs/r_1 1.88; first radial cell obliterated, second radial cell narrow, slightly longer than first (1.29: 1) (Fig. 5E); fmcu under slightly beyond middle of second radial cell; m_{3+4}/cu_1 1.97.

Abdomen brown. Spermathecae (Fig. 5H) two, subequal, oval, with short ducts, measuring 69μ x 51.75μ and 58.65μ x 43.13μ.

Adult Male.-

Length 1.58 mm. Wing (Fig. 5K) 0.96 x 0.30 mm. Color as in female.

Antenna (Fig. 4J) with segment 3 and 4 about as long as wide, segments 5-10 longer than wide and segments 11-14 elongate; AR 1.01 (0.99-1.02). Maxillary palp (Fig. 5I) somewhat slender, with third segment long and swollen at third and bearing small, shallow sensorium; last two segments united broadly at joint as in female; PR 3.85.

Thorax with scutellum bearing eight large bristles (Fig. 5M). Legs light brown; TR 1.06 in fore leg, 0.56 in middle leg and 0.74 in hind leg; hind tibial comb bearing eight bristles.

Wings brown, CR 0.44. Venation : vLR 1.05: 1: 2.19; rs/r_1 1.38; first radial cell completely obliterated, second radial cell small, moderately wide; RR 0.50; fmcu under about middle of wing from arculus to tip along costa; m_{3+4}/cu_1 2.43.

Genitalia (Fig. 5N): ninth sternite 0.84 as long as wide; ninth tergite 0.47 as long as wide; parameres with basimere 1.69 as long as wide and telomere 4.44 as long as wide; aedeagus V-shaped, shorter than width at base (0.76: 1) with lateral edges more heavily sclerotized and tip pointed; claspettes the usual slender arch with b/c/b in proportion of 1.38: 1: 1.38.

Holotype (fourth instar larva).- Collected from decaying grass at Wallace Way, Singapore in May 1962. Deposited in Lyman Entomological Museum, Macdonald College, Quebec.

Paratypes.- Collected from same locality as holotype; 1 pupa, 62 females and 60 males in personal collections.

P. clara is close to P. sauteri (Kieffer)(Tokunaga and Murachi, 1959) in structure of the male genitalia but differs from the latter in the pointed tip of the aedeagus and the narrower base of the telomere and more slender claspettes. The tarsal ratios of fore and hind legs are significantly smaller in the male of this species, 1.06 and 0.56 respectively to 1.2 and 0.76 in sauteri.

Comparison with the immature stages of sauteri is not possible since Tokunaga has not collected nor described these stages.

P. clara also resembles P. ingrami (Carter) (1919) from West Africa, Indonesia, Malaya, British West Indies, Marquesas Is., and Hawaii in structure of the male genitalia, but from the description of Hardy (1960) for Hawaiian specimens, differs from ingrami in a number of characters: the male antennal segment 12 (Macfie's 13th segment) is much shorter than the last two segments combined instead of almost equal as in ingrami; the tarsal ratios of the fore, middle and hind legs are, respectively, 1.06, 0.56 and 0.74 instead of about 1.5, 1.0 and 1.0 respectively, in ingrami; the female is a much smaller species measuring 1.3 mm. for body length and 0.78 mm. for wing length against 1.5-1.7 mm. and 1.4-1.6 mm. respectively for the Hawaiian ingrami.

Carter's (1919) original descriptions and figures show clearly that ingrami differs from this species distinctly in pupal characters; there are only four pairs of tubercles on the cephalothoracic dorsum instead of six in ingrami and the innermost pair of tubercles on the dorsum of the abdominal segments are simple and not torch-like.

Proforcipomyia pennielongata CHAN NEW SPECIES

Larva.-

Length of full grown fourth instar 3.15 mm. Color (preserved) pale white, without pigments.

Head light brown, not markedly scalloped; p hairs spear-shaped, q hairs small, spoon-shaped, all other hairs simple (Fig. 6B). HR 1.60; OH/v 1.47; pq/qt/pt 1.14: 1: 2.16; tt/ant 0.44; qq/eyes 0.29; qq/ss 0.28; pp/ant 1.05.

Chaetotaxy on first ten body segments similar, each segment with the usual spear-shaped a hairs, five pairs fine lateral hairs and one pair minute ventral seta, the latter compound in the thoracic segments and simple in the abdominal. Segment 8 with only three pairs of lateral setae; segment 9 as figured (Fig. 6A). Prothoracic pseudopod the usual spinulose cushion, the anterior end with about 15 stronger hooklets; length, width and depth in proportion of 1.62: 1: 1.18. Posterior pseudopod (Fig. 6D) bearing a posterior row of eight long black hooklets and an anterior row of ten smaller hooklets; anal blood gills four, pointed. Cauda long, tapering, fringed laterally with minute setae, slightly longer than last abdominal segment.

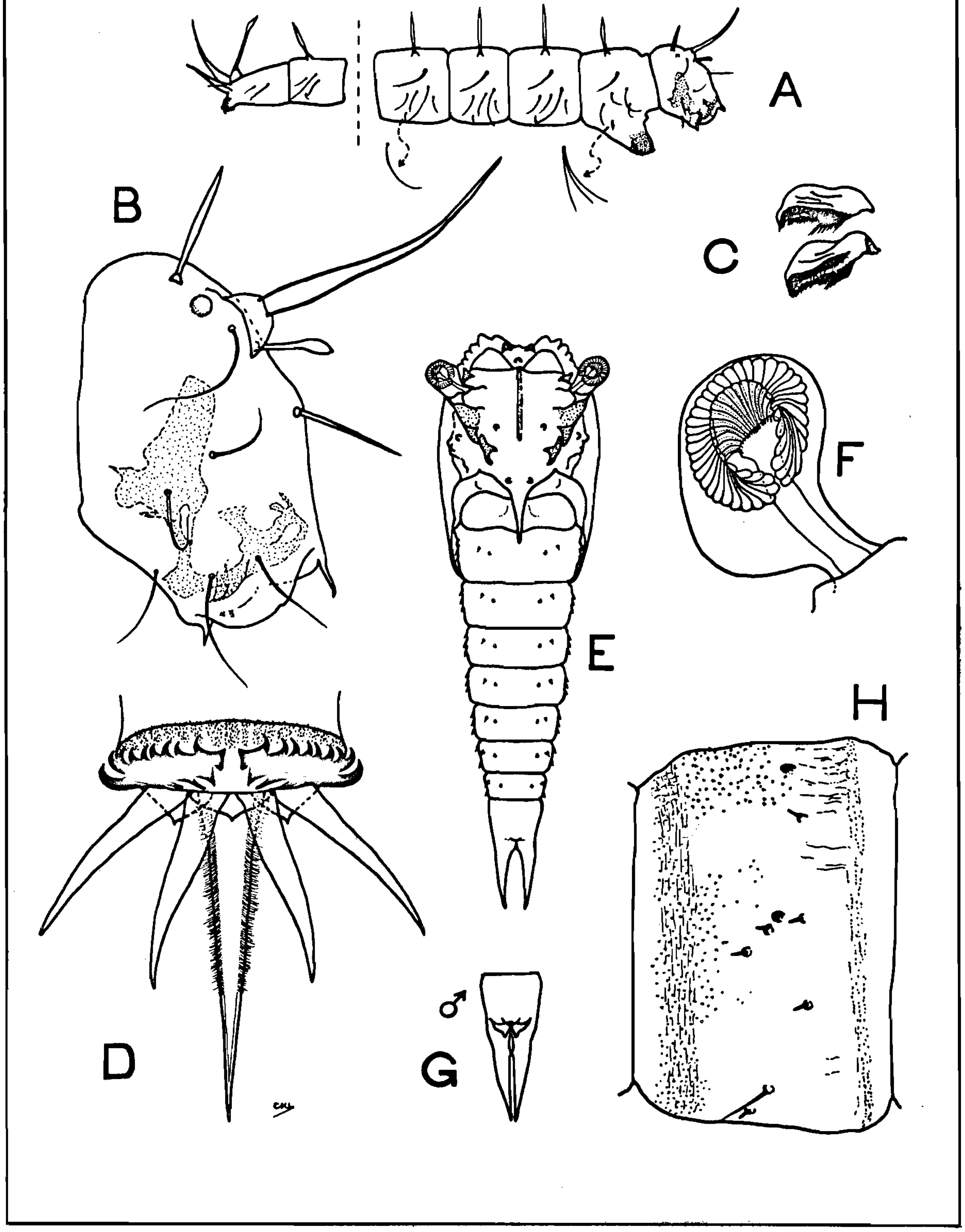
Pupa.-

Length 2.58 mm. in female and 2.66 (2.63-2.69) mm. in male. Color

Fig. 6. Proforcipomyia pennielongata n. sp.

- A-D, Fourth-instar larva:
  - A, Larva, lateral view
  - B, Head
  - C, Mandibles
  - D, Posterior pseudopod
- E-H, Pupa:
  - E, Female, dorsal view
  - F, Prothoracic horn
  - G, Last segment, dorsal view
  - H, Fifth abdominal segment, lateral view

Fig. 6



dark brown, same as that of substratum, thorax darker brown.

Head bearing three tubercles on median head sclerite; lateral sclerites devoid of tubercles. Cephalothorax length to width 1.60 in female and 1.72 (1.67-1.76) in male; ratio of length of head to thorax 0.35 in ventral aspect and 0.11 in dorsal aspect in female and respectively 0.40 (0.39-0.41) and 0.15 (0.13-0.16) in male.

Thorax bearing median ridge anteriorly and six pairs of tubercles on dorsum, largest pair just posterior to respiratory horns and bearing short seta apically and tubercle-like projection posteriorly. Prothoracic horn (Fig. 6F) trumpet-shaped, with twenty-two spiracular papillae on upper palisade and 36 in lower palisade in female and respectively 23 and 39.33 (38-42) in male, the spiracular papillae forming an almost spherical ring; horn 1.57 times its width in female and 1.57 (1.47-1.62) in male; tracheal length to horn length 0.77 in female and 0.73 (0.73-0.75) in male.

Abdominal segments 3-7 similar in chaetotaxy, each with two pairs of dorsal tubercles, five pairs lateral and two pairs ventral (Fig. 6H); segments 2 and 8 also each bearing two pairs of dorsal tubercles but segment 8 bears only two pairs lateral and two pairs ventral while segment 2 bears three pairs lateral and lacks ventral tubercles. Terminal processes sharply pointed, divergent in female and closely appressed in male (Fig. 6G), the inner edge at basal third touching by slight inward-growing projections of either processes; length, width and depth in proportion of 4.19: 1.50: 1 in female and respectively 4.97 (4.76-5.28): 1.28 (1.21-1.39): 1 in male. Male sexual processes dorsal, small, short, with length, width and depth in proportion of 2.96 (2.53-3.17): 2.95 (2.67-3.17): 1.

Larval exuviae not retained.

Adult Female.-

Length about 1.5 mm. Wing (Fig. 7C) 1.02 x 0.42 mm.

Head with antennae and mouthparts brown, eyes dark. Antenna (Fig. 7A) with segment 3 as long as wide, segments 4-9 longer than wide and last five segments elongate; sensilla in segments 2-9 slender, as long as respective segments bearing them; AR 1.10. Maxillary palp (Fig. 7B) slender, third segment longest; bearing shallow, sensorium with irregular outline at basal swollen third; segments in proportion of 13: 17: 39: 21: 13; PR 3.81.

Thorax brown. Legs lighter brown; TR 1.00 in hind leg; hind tibial comb bearing five bristles. Wings brown; CR 0.53.

Spermathecae (Fig. 7E) two, subequal, oval, measuring 68.09 x 57.23 μ and 54.26 x 42.55 μ.

Adult Male.-

Length 1.80 mm. Wing (Fig. 7H) 1.08 x 0.35 mm. Color as in female.

Antenna (Fig. 7F) with segments 3-4 about as long as wide, segments 5-10 longer than wide and segments 11-14 elongate, segment 11 longest; AR 0.92. Maxillary palp (Fig. 7G) slender, segment 3 longest but not wider than the rest, and bearing scattered sessile sensilla on swollen basal portion; segments in proportion of 9: 10: 28: 14.5: 9; PR 4.67.

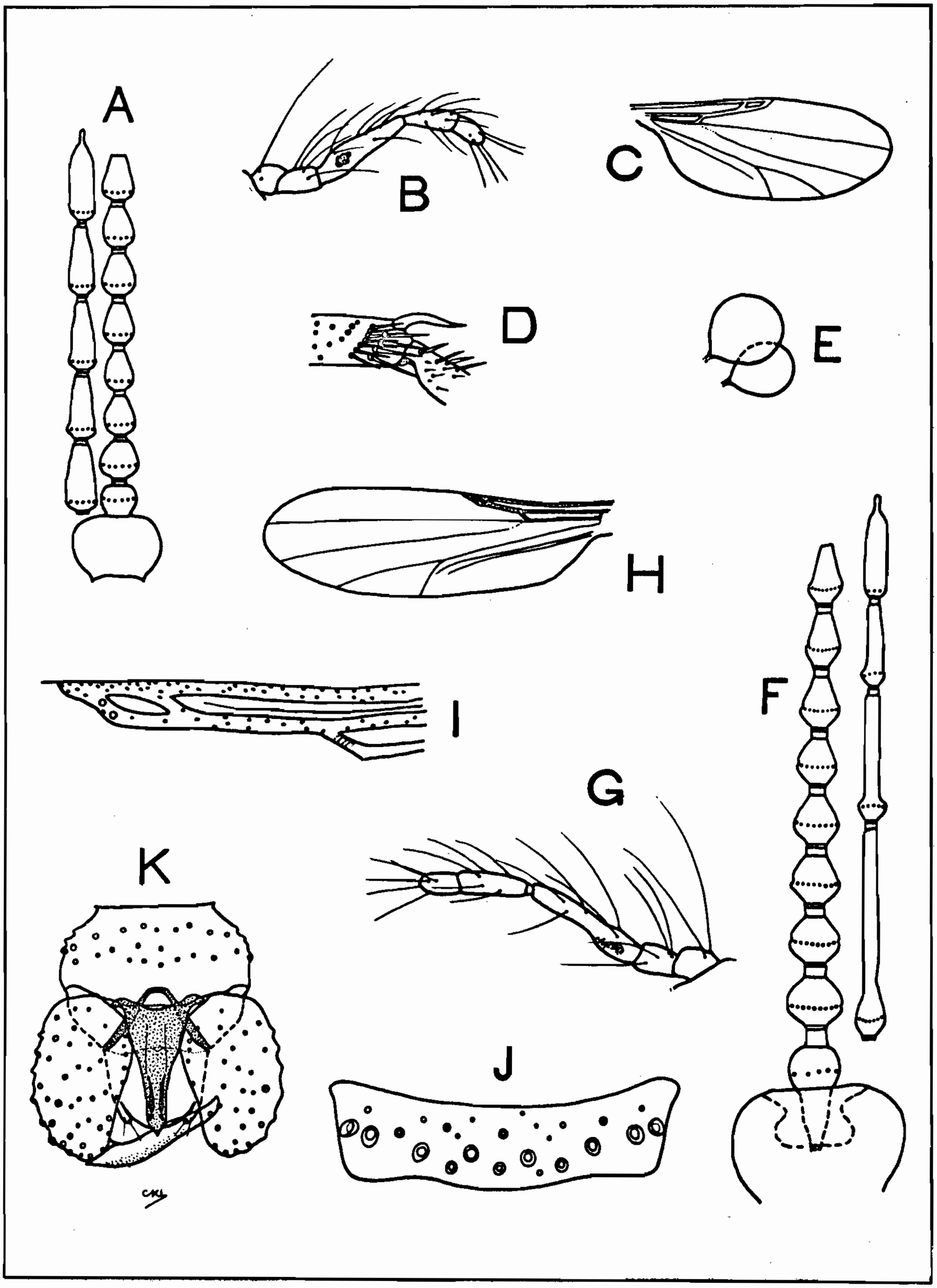
Thorax light brown with scutellum bearing 11 large bristles in row across posterior margin (Fig. 7J). Legs light brown, TR 1.10 in fore leg, 0.44 in middle leg and 0.73 in hind leg; tibial comb of hind leg bearing seven bristles.

Wings brown, CR 0.42. Venation: vLR 1.07: 1: 2.23; rs/r_1 1.53; first radial cell completely obliterated, second radial cell small, elliptical (Fig. 7I), RR 0.42; fmcu under beyond end of costa; m_{3+4}/cu_1 2.42.

Fig. 7. *Proforcipomyia pennielongata* n. sp.

- A-E, Adult female:
  - A, Antenna
  - B, Maxillary palp
  - C, Wing
  - D, Hind tibial comb
  - E, Spermathecae
- F-K, Adult male:
  - F, Antenna
  - G, Maxillary palp
  - H, Wing
  - I, Anterior wing venation
  - J, Scutellum
  - K, Genitalia

Fig. 7



Genitalia (Fig. 7K): ninth sternite 0.58 as long as wide; ninth tergite 0.75 as long as wide; parameres with basimeres wide basally, tapering to narrow apical end, 1.76 times as long as basal width, and with telomeres boat-shaped, curved and pointed apically, 5.60 times as long as greatest width; aedeagus narrowly shield-shaped, much longer than basal width (1.53: 1) and bearing near caudal tip two heavily sclerotized peg-like carinae; claspettes a slender, tall arch with basal arms, basal union in proportion of 3.00: 1: 3.00.

Holotype (adult male).- Reared from larvae collected from a heap of decaying lallang (Imperata cylindrica Beauv. Agrost) and leaves at Wallace Way, Singapore in June 1962.

Paratypes.- 10 larvae, 10 pupal exuviae, 10 males and 4 females in personal collections. Collected from same locality and habitat as holotype.

This species is distinct from all other species recorded and described in the presence of peg-like carinae at the tip of the aedeagus and in the very long, shield-shaped aedeagus, of the male genitalia.

Other species.-

Species described in all stages include the following:

bromeliae (Saunders) (1956); Can. J. Zool. 34: 665
falcifera (Saunders) (1959); Can. J. Zool. 37: 39
ingrami (Carter) (1919); Ann. Trop. Med. Parasitol. 12: 290
longispina (Saunders) (1956); Can. J. Zool. 34: 669
mortuifolii (Saunders) (1959); Can. J. Zool. 37: 35
phlebotomoides (Bangerter) (1933); Konowia 12: 252
setigera (Saunders) (1959); Can. J. Zool. 37: 38
spatulifera (Saunders) (1956); Can. J. Zool. 34: 667
wirthi (Saunders) (1956); Can. J. Zool. 34: 663

As suggested by Saunders (1959), Proforcipomyia can be divided into groups on the basis of larval and pupal characters. Four groups are separated:

Group 1

Larvae with long tail setae and compound hairs on head and tail. Pupae with setigerous tubercles on thorax and terminal processes are attenuated. Three species included: setigera, longispina and phlebotomoides.

Group 2

Larvae with terminal hooklets on prothoracic pseudopod. Pupae highly tuberculate and with complete circle of spiracular papillae in respiratory horn. Two species: falcifera, bromeliae.

Group 3

Larvae with dorsal paired setae spatulate. Pupa with ringed tubercles on dorsum of abdomen. One species: spatulifera.

Group 4

Other species.

These groups may provide a basis for the establishment of subgenera when more material becomes available.

C. GENUS CALOFORCIPOMYIA SAUNDERS (1956)

Type species caerulea Saunders (1956)

1. DIAGNOSIS

The following diagnosis of the immature stage is taken from Saunders (1956) "Revision of the genus Forcipomyia":

"Larva.- Cylindrical, more elongate than subgenus Forcipomyia larvae. Head strongly hypognathous, with long, forward-curving p hairs. Prothoracic pseudopod a simple spinulose cushion. Chaetotaxy of body: each normal segment bears dorsal a hairs; dorsolateral hairs arbitrarily homologized with c hairs of subgenus Forcipomyia, in which case b and d hairs are absent;

two fine lateral hairs, probably e and f. Last abdominal segment bearing a large dorsal chitinous process extending up and back beyond cauda and anal gills, with two basal and two long terminal stout chaetae. Cauda moderately long and pointed, much like that of subgenus Proforcipomyia without the lateral fringe of short hairs. Anal blood gills two, bifid. Anal pseudopod normal.

Pupa.-

Relatively spineless, with a prominent pair of setigerous processes, conical at base, on dorsum of thorax just above and behind the prothoracic horns. Abdominal setae few, very small, no different on last segments, which retain the larval exuviae. Terminal abdominal processes in both sexes greatly attenuated, making the last segment equal to or longer than the three preceding segments together. Male sexual processes dorsal. Prothoracic horns slender, with row of spiracular papillae across extremity, not greatly different from those of some species in the subgenus Forcipomyia."

Adult Female.-

Medium-sized or small. Thorax and abdomen with subcutaneous indigo-blue pigmented granules. Maxillary palp with last two segments completely segmented or fused and segment 3 with sensorium or scattered sensilla. Antenna with basal flagellar segments elongate, two to three times as long as wide and with hyaline sensory hairs as long as segments. Legs banded by dark scales; claws and empodia normal. Wings usually with scales on costal and radial cells, unmarked or adorned with dark and pale spots; costa reaching well beyond middle of wing; second radial cell opened and elongate, first radial cell slit-like. Two spermathecae.

Adult Male.-

Same as female with usual sexual differences. Hypopygium with claspettes V-shaped, pointed at middle; sternite 9 transverse or subsquare and usually without caudal emargination.

Species described in all stages

caerulea (Saunders)(1956), Can. J. Zool. 34:681

varicolor (Saunders)(1956), Can. J. Zool. 34: 683

Species described in adult stages

Species attributable to this genus on adult characters include:

squamianulipes Tokunaga and Murachi (1959), Insects of Micronesia 12(3): 194

takahashii Tokunaga (1940), Tenthredo 3: 88

According to Saunders (1956) the following two species in all probability belong to the genus Calofcrcipomyia:

auripes Ingram and Macfie (1924), Ann. Trop. Med. Parasitol. 18: 560

pluvialis Malloch (1923), Entomol. News 34: 4

D. GENUS METAFORCIPOMYIA SAUNDERS (1956)

Type species cerifera Saunders (1956)

DIAGNOSIS

Saunders' (1956) diagnosis is reproduced as follows:

"Larva .- Cylindrical, in general form like larvae of subgenus Forcipomyia, but with knob-like chaetae on head and body bearing tubes and cones of white wax and liquid globules powdered with wax. Antennae situated on long socles like many Atrichopogon larval antennae. Prothoracic pseudopod a coarsely spinose cushion. Anal pseudopod normal. Cauda short, lobose.

Pupa.- Practically devoid of chaetae; thorax with an anterior pair of slender, spinulose, setigerous processes and four other low spinulose processes. Prothoracic horns slender, with row of spiracular papillae over top to halfway down stem. Larval exuviae retained. (This diagnosis subject to modification when more species of the subgenus are found).

Adults.- TR 2.0. Basal flagellar segments of female antenna flask-shaped, each with one hyaline sensory hair twisted diagonally around segment; segments 9-13 no longer, but last three stout. Palpal segments 4 and 5 fused inseparably. Costa reaching barely to middle of wing; first radial cell narrowly open, second open, short; vein M2 absent. Spermathecae two. Male genitalia with curved basistylar apodemes joined in a square-topped arch, with parameres (claspette processes) fused in mid-line, extending back to tip of aedeagus."

Species described in all stages

Forcipomyia (Metaforcipomyia) cerifera Saunders (1956),
Can. J. Zool. 34: 685

Other species recorded

M. fuscimaculata (Hardy)(1960), Hawaii, but this species is a Schizoforcipomyia.

E. GENUS FORCIPOMYIA MEIGEN (1818)

1. DIAGNOSIS

Larva.-

Elongate, cylindrical, segmentally constricted. Head prognathous or hypognathous; antennae normal, with short socle[1](i.e. tubercle) and moderately long filament tapering to pointed tip. Body chaetae variable in number and size, most simple, some bifid or multiple; a hairs spear-shaped. Prothoracic pseudopod abruptly conical or medially divided into two lobes. Anal blood gills two, double or

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[1] The term "socle" has been adopted from Nielsen (1951), subsequently used by Ewen and Saunders (1958), Saunders (1959, 1964) and Chan and Saunders (1965) as a valid and concise name for the antennal base.

four, inner pair single. Cauda short, bluntly conical or more tapering, finely setulose.

Pupa.-

Cuticular processes on cephalothorax and abdomen variable in number and size. Prothoracic respiratory horns narrow or broad and projecting at base, with or without narrow neck, distal knob not swollen or more or less swollen, with row of spiracular papillae curving over it. Male sexual processes dorsal on last abdominal segment. Larval exuviae retained on last 3-5 segments or not retained.

Adult Female.-

Small to rather large; more or less hairy, with pale coloration or with scales and colored markings variously developed, especially on legs and wings. Antennae 14-segmented, segments 2-9 pyriform or vasiform, with hyaline sensory hairs; segments 10-14 abruptly or gradually elongate. Palpal segments 4 and 5 distinct or partially or completely fused; segment 5 with distinctly chitinised common sensorium or with a group of capitate sensilla without enclosing chitinous ring. Wings thinly or thickly clothed with macrotrichiae; costa hardly reaching middle wing or to two-thirds length of wing; second radial cell short or elongated, open or closed or almost closed. Hind TR usually more than 1.3 in one group or less than 1.33 in the rest; empodia well-developed. One or two spermathecae.

Adult Male.-

As in female with usual sex differences. Male genitalia with aedeagus typically shield-shaped or a V or T with sclerites at apex; claspettes with or without backwardly-directed processes, with or without basal union.

2. KEY TO SUBGENERA OF FORCIPOMYIA (LARVA)

1. Head prognathous, prothoracic pseudopod abruptly conical, transversely ridged and finely setulose, bearing three pairs long, curved, hyaline hooklets at tip and three pairs short, black hooklets and one pair short sinuous processes in middle........................Warmkea

Head hypognathous, prothoracic pseudopod medially divided, a crown of hooklets on each half....................2

2(1). Anal pseudopod undivided, a transverse ridge with two rows of hooklets...............................Forcipomyia

Anal pseudopod divided into two lobes, each lobe hook-crowned...............................Schizoforcipomyia

KEY TO SUBGENERA OF FORCIPOMYIA (PUPA)

1. Body with knobby and spiny processes; prothoracic horns broad at base, projecting to angular knob on posterior surface, neck narrow, head rounded with many spiracular papillae in row over top; larval exuviae not retained.............................Warmkea

Body usually not knobby or spiny; prothoracic horns typically narrow at base, neck typically not narrow and distinct, head narrow or more or less swollen, with row of spiracular papillae curving over it; larval exuviae retained on last 3-5 segments...2

2(1). Prothoracic horns very short; thorax and all first seven abdominal segments bearing long processes....Schizoforcipomyia

Prothoracic horns relatively longer; thorax with low tubercles or long processes; abdominal segments never with all first seven segments bearing long processes..............................Forcipomyia

KEY TO SUBGENERA OF FORCIPOMYIA (ADULT FEMALE)

1. Wing costa reaching to two-thirds length of wing, second radial cell elongate; maxillary palpal segments 4 and 5 partially or completely fused; spermatheca one....................................Warmkea

Wing costa not reaching to two-thirds length of wing; second radial cell short; maxillary palpal segments 4 and 5 distinct or fused; spermatheca one or two...2

2(1). Maxillary palpal segment 5 distinctly longer than 4; segments 4 and 5 completely segmented or completely fused; one or two spermathecae.................................. *Schizoforcipomyia*

Maxillary palpal segment 5 distinctly shorter than 4 or about equal or rarely slightly shorter than 4; segments 4 and 5 completely segmented; two spermathecae............... *Forcipomyia*

KEY TO SUBGENERA OF *FORCIPOMYIA* (ADULT MALE)

1. Genitalia with aedeagus in the form of a V or T, bearing outward-turning sclerites at apex; claspettes with or without processes......... *Schizoforcipomyia*

Genitalia with aedeagus typically shield-shaped, without outward-turning sclerites at apex; claspettes always with processes..................................2

2(1). Max. palpal segments 4 and 5 partially or completely fused.. *Warmkea*

Max. palpal segments 4 and 5 distinct................... *Forcipomyia*

3. SUBGENUS *FORCIPOMYIA* S. STR. MEIGEN (1818)

Subgenus type *bipunctata* (Linnaeus) (1767)

DIAGNOSIS

Larva.-

Head hypognathous, profile smoothly rounded. Body chaetae many, rarely long; *a* hairs typically spear-shaped, hygroscopic. Prothoracic pseudopod medially divided, a crown of hooklets on each half. Anal pseudopod a transverse ridge bearing two rows of hooklets. Anal blood gills two, each bluntly bilobed.

Pupa.-

Cuticular processes and spines on body variable in number and size, when long never borne on all first seven abdominal segments. Prothoracic horns swollen, bearing row of spiracular papillae curving over it.

Adult Female.-

Small to rather large, typically with colored markings variously developed on wings and legs. Antennal segments 2-9 flask-shaped, with more or less well-developed neck parts, never compressed, with two hyaline sensory hairs; segments 10-14 typically elongate, segment 10 as long as 9 or longer. Maxillary palp almost always distinctly five-segmented and palpal segment 3 with distinct chitinised sensorium. Wings densely clothed with macrotrichia, no bare areas along veins; costa reaching near or at middle of wing or to three-fifths of wing; first radial cell present or absent, second radial cell short. Hind TR less than 1.33. Two spermathecae.

Adult Male.-

As in female with usual sexual differences. Genitalia with typically shield-shaped aedeagus, variable in form but never in form of V or T with sclerites at apex; claspettes always with processes arising from basal union or when basal union is absent, from tips of basal arms.

Forcipomyia (Forcipomyia) bikanni CHAN NEW SPECIES

The writer takes great pleasure in naming this species after Dr. Lawrence Lau Bik Ann in appreciation of the help and inspiration he has given.

Larva.-

Length of full-grown fourth instar (Fig. 8A) 4.20 mm. Color pale brown with intestinal contents brown.

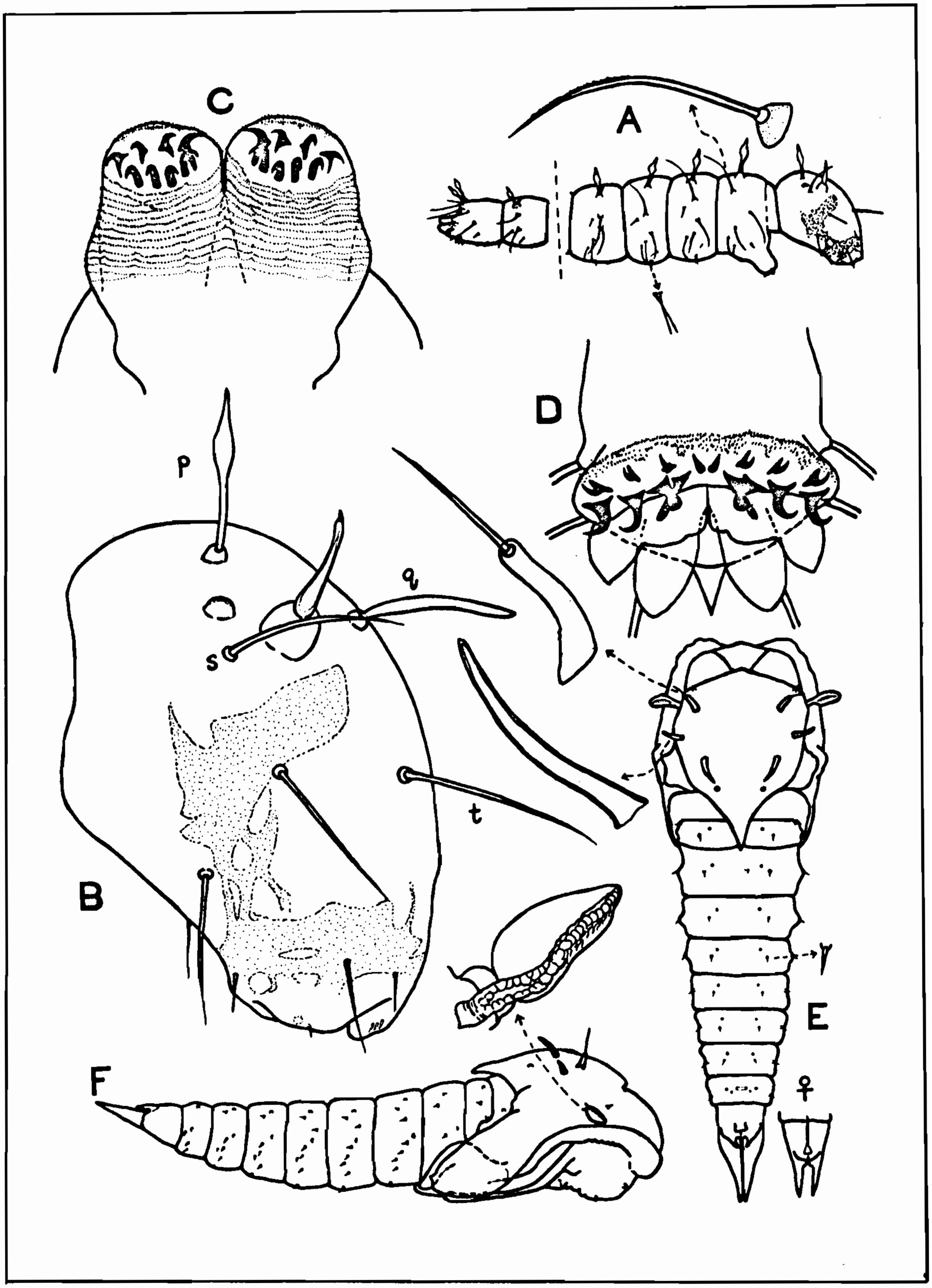
Head (Fig. 8B) dark brown, p hairs spear-shaped, q hairs sword-shaped, curved; antennae long, tapering to pointed tip; HR 1.52; AR 2.39; qt/ts/sq in proportion of 1.05: 1.50: 1; tt/antennae 0.49; qq/eyes 0.24; qq/ss 0.22. Eyes small and low.

Prothoracic a setae spear-shaped, b setae filamentous and long; prothoracic pseudopod (Fig. 8C) bifid at apical end, each branch bearing

Fig. 8. _Forcipomyia_ (_Forcipomyia_) _bikanni_ n. sp.

- A-D, Fourth-instar larva:
  - A, Larva, lateral view
  - B, Head
  - C, Anterior pseudopod
  - D, Anal pseudopod
- E-F, Pupa:
  - E, Pupa, dorsal view
  - F, Pupa, lateral view

Fig. 8



at apex a ring of eight dark brown hooks; its length, width and depth in proportion of 2.09: 2.51: 1.

Chaetotaxy as illustrated (Fig. 8A), similar in abdominal segments 1-7; a setae spear-shaped and hygroscopic, other setae filamentous as figured.

Abdomen with posterior pseudopod (Fig. 8D) bearing anterior row of eight small, curved hooklets and posterior row of eight large, curved hooklets; anal blood-gills two pairs, bilobed. Cauda short, pointed.

Pupa.-

Length 2.18 mm. in female and 3.30 mm. in male. Color pale yellow, darker yellow in thorax but turning dark just prior to adult emergence. Pupa retaining larval exuviae in last three segments.

Head sclerites without tubercles. Cephalothorax 1.75 times longer than its greatest width in female and 1.43 times in male. Head length to thorax length 0.35: 1 in dorsal aspect and 0.59: 1 in ventral aspect in female and respectively 0.29: 1 and 0.48:1 in male.

Thorax bearing four pairs of tubercles on dorsum (Fig. 8E), the anteriormost with a seta 1½ times length of elongate tubercle, the second and third pairs non-setate, elongate and the posteriormost pair only rudimentary. Prothoracic horn short, spindle-shaped, with short pedicel and bearing about 20 spiracular papillae running antero-dorsally from apex to base; horn length to width 2.43:1 in female and 2.38: 1 in male; tracheal length about equal to horn length in both sexes.

Abdomen with chaetotaxy as shown (Fig. 8E, 8F). Segments 1 and 2 each with three pairs small tubercles, antero-dorsal pair rudimentary; segments 3-7 each with a pair of spiracles and seven pairs of tubercles of which two pairs are dorso-median, four pairs lateral and one pair ventral;

segment 8 with two pairs non-setate dorso-median, two pairs lateral and one pair ventral. Terminal processes on last segment longer and appressed in male, shorter and divergent in female, tapering gradually to tip in both sexes. Male sexual processes small and dorsal.

Adult Female.-

Length 1.99 (1.73-2.25)/9* mm. Wings (Fig. 9D) 0.99 (0.83-1.08)/10 mm. by 0.43 (0.39-0.50)/10 mm.

Head with mouthparts dark-brown, antennae except pedicels and scapes light brown, eyes dark, separated at vertex by narrow slit. Maxillary palp (Fig. 9B) large, five-segmented, with third segment broad at basal half and narrow at distal half and with PR 2.63 (2.35-2.80)/10. Antennae (Fig. 9A) uniformly light brown from segments 2-14; AR 0.69 (0.61-0.80)/10. Hairs on vertex long, forwardly directed.

Thorax dark brown with scutellar bristle arrangement as shown (Fig. 9K). Legs pale brown, hind legs with femur and tibia bearing two dark brown patches near femo-tibial joint, the former the larger; TR 1.26 (1.23-1.33)/9 in fore leg, 0.94 (0.88-0.96)/9 in middle leg, and 0.85 (0.79-0.89)/10 in hind leg; apical tibial comb with eight to ten bristles (Fig. 9C).

Wings pale brown, densely covered with brown, almost scale-like hairs, especially on costa and fine, rather long hairs over entire surface; CR 0.46 (0.44-0.48)/10. Venation: vLR 1.14 (1.09-1.21): 1: 1.86 (1.73-1.99)/10; rs/r_1 1.56 (1.48-1.67)/10; first radial cell obliterated, second radial cell moderately wide, slightly longer than first (1.02 (0.70-1.27): 1/10) (Fig. 9E); m_{3+4}/cu_1 1.81 (1.73-1.90)/10;

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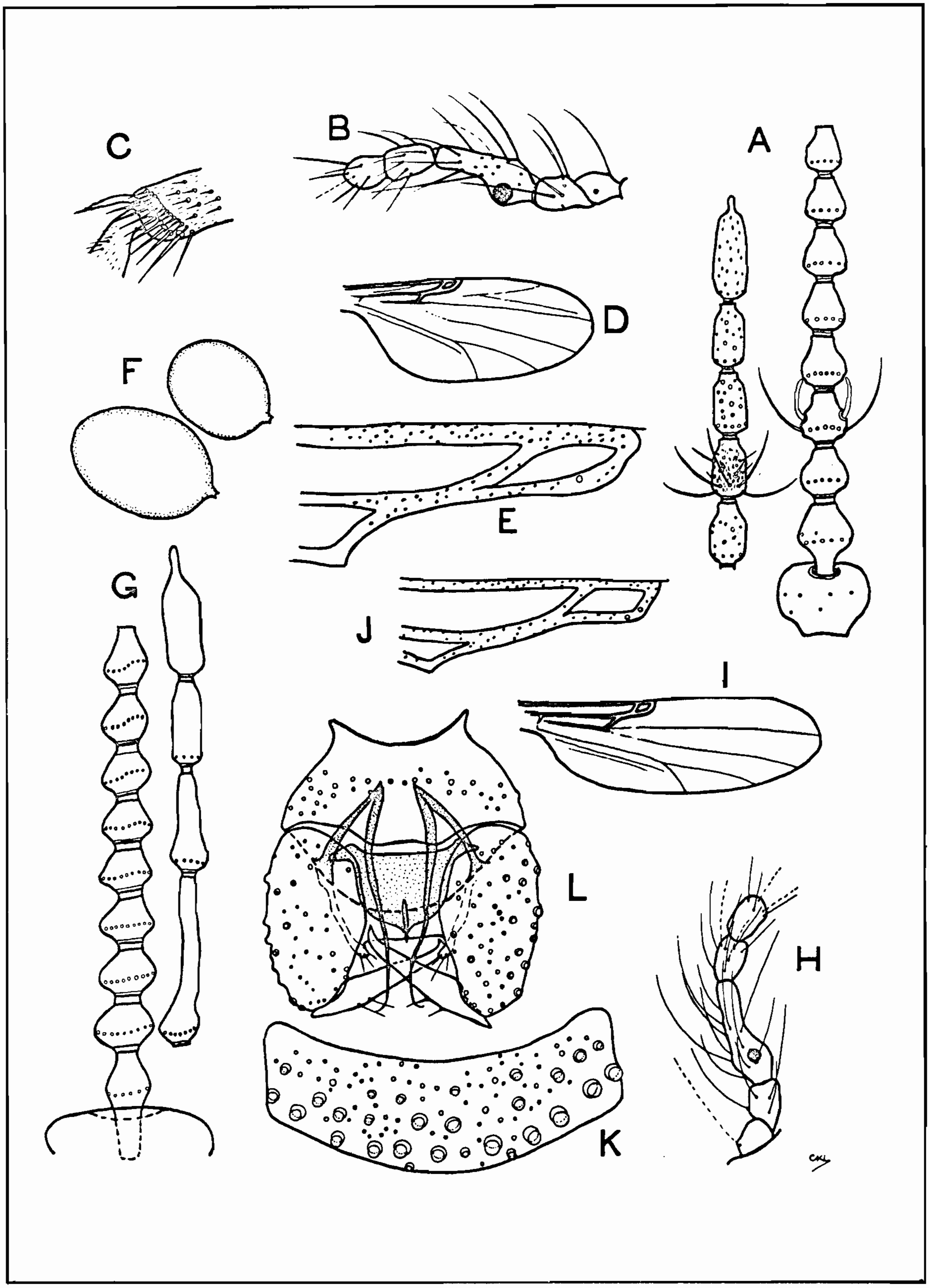
* mean (range)/no of specimens measured

Fig. 9. *Forcipomyia* (*Forcipomyia*) *bikanni* n. sp.

- A-F, Adult female:
  - A, Antenna
  - B, Maxillary palp
  - C, Hind tibial comb
  - D, Wing
  - E, Anterior wing venation
  - F, Spermathecae
- G-L, Adult male:
  - G, Antenna
  - H, Maxillary palp
  - I, Wing
  - J, Anterior wing venation
  - K, Scutellum
  - L, Genitalia

Fig. 9



tip of fmcu under about end of costa (Fig. 9D). Halteres light brown.

Abdomen brown, covered with dense, thick hairs. Spermathecae (Fig. 9F) two, unequal, oval, measuring 133.86 (117.30-148.35)/10 µ by 88.15 (75.90-96.60)/10 µ in the larger and 98.33 (82.80-117.30)/10 µ by 68.48 (62.10-75.90)/10 µ in the smaller.

Adult Male.-

Length 2.05 (1.88-2.18)/4 mm. Wings (Fig. 9I) 0.99 (0.93-1.07)/4 mm. by 0.35 (0.32-0.36)/4 mm. Color as in female.

Antenna (Fig. 9G) with AR 1.01 (0.97-1.08)/4. Maxillary palp (Fig. 9H) distinctly five-segmented, PR 3.30 (3.06-3.50)/4.

Thorax with color of legs as in female. TR 0.96 (0.83-1.08)/4 in fore leg, 0.75 (0.72-0.78)/4 in middle leg and 0.71 (0.67-0.74)/4 in hind leg; apical tibial comb with eight or nine bristles.

Wings (Fig. 9I) with CR 0.43 (0.42-0.43)/4. Venation: vLR 1.13 (1.11-1.14): 1: 1.89 (1.86-1.96)/4; rs/r_1 1.59 (1.39-1.82)/4; first radial cell obliterated, second radial cell moderately wide, 0.92 (0.83-1.20)/4 times longer than first (Fig. 9J); fmcu under slightly beyond tip of costa.

Abdomen light brown with genitalia darker brown. Genitalia (Fig. 9L): sternite 9 about half as long as wide (0.45 (0.40-0.54): 1/4); tergite 9 more than half as long as wide (0.62 (0.56-0.69): 1/4). Basimeres large, broad, about twice as long as wide (1.98 (1.87-2.10):1/4); telomeres 0.82 (0.77-0.88): 1/4 times shorter than basimeres, gradually tapering to curved narrow pointed tip and 5.58 (5.39-5.92)/4 times as long as wide. Aedeagus shield-shaped, large, length at base shorter than width (0.67 (0.65-0.69): 1/4) and bearing at apex a median sharp point; claspettes widely separated at base, basal arms bearing apically a backwardly-directed process reaching to tip of basimeres.

Holotype (fourth instar larva).- Collected under decaying leaves in September, 1961, at Wallace Way, Singapore. Deposited in Lyman Entomological Museum.

Paratypes.- 19 larvae, 8 pupae, many males and females in personal collections. Collected from same locality, and habitat.

Forcipomyia (Forcipomyia) bipunctata propinqua CHAN NEW SPECIES

Larva.-

Length of full grown fourth instar (Fig. 10A) 4.26 ± 0.33 mm. Color in life whitish yellow.

Head yellowish brown; eyes, antennae and setae as in Fig. 10B. HR 1.71 ± 0.04; AR 2.59 ± 0.25; qt/ts/sq in proportion of 1.74 ± 0.15: 1.90 ± 0.20: 1; tt/ant 0.46 ± 0.02; qq/eyes 0.25 ± 0.02; qq/ss 0.24 ± 0.01.

Prothoracic a and b setae with filament and tubercle in proportion of 8.22 ± 0.57 and 12.89 ± 0.48 respectively; prothoracic pseudopod (Fig. 10C) bifid, with length, width and depth in proportion of 2.61 ± 0.24: 1.85 ± 0.18: 1 and bearing on apex of each branch six black, backward-directed hooks and three weak central ones.

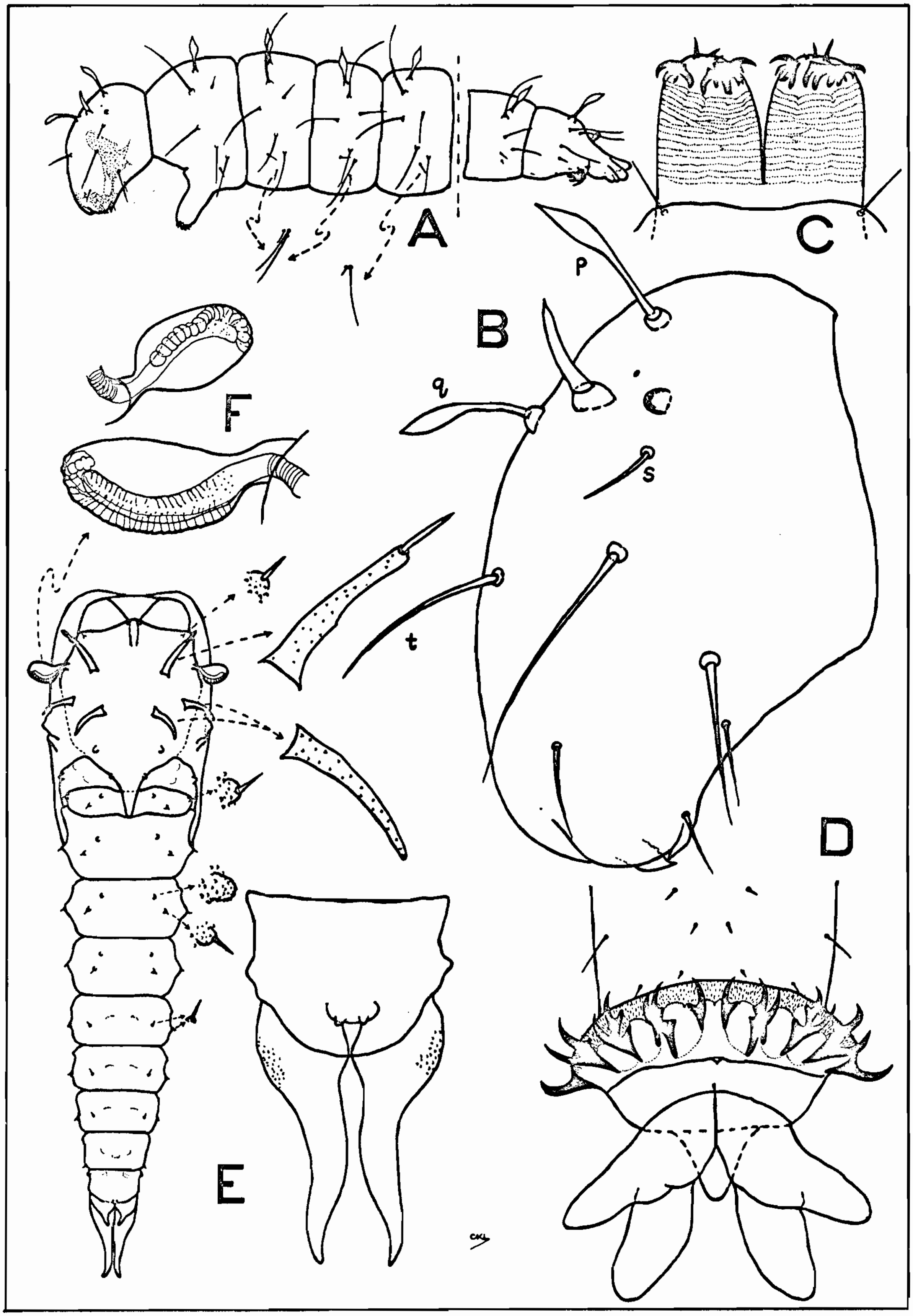
Chaetotaxy on abdominal segments 1-7 similar (Fig. 10A) and that on segments 9 and 8 as figured (Fig. 10A, Fig. 10D). Anal pseudopod (Fig. 10D) armed with two rows of four hooks each on either side of median line; anal blood gills two, bilobed; cauda short, conical. In full-grown larva near pupation, abdominal segments 1-8 bear a transverse cuticular bar connecting the bases of the a hairs.

Cuticular armature confined to dorsum and dorsal half of pleura

Fig. 10. _Forcipomyia_ (_Forcipomyia_) _bipunctatapropinqua_ n. sp.

A-D, Fourth-instar larva:
  A, Larva, lateral view
  B, Head
  C, Anterior pseudopod
  D, Anal pseudopod
E-F, Pupa:
  E, Pupa, dorsal view
  F, Prothoracic horn

Fig. 10



consisting of minute hooks; ventral integument smooth.

Pupa.-

Length 2.29 ± 0.21 mm. in female and 2.48 ± 0.17 mm. in male. Color as in larva but dark brown just prior to emergence of adult.

Head sclerites devoid of tubercles. Cephalothorax 1.71 ± 0.08 times longer than its greatest width in female and 1.81 ± 0.07 in male. Head to thorax 0.23 ± 0.03: 1 in dorsal aspect and 0.45 ± 0.03: 1 in ventral aspect in female and respectively 0.27 ± 0.03 : 1 and 0.43 ± 0.03 : 1 in male.

Thoracic dorsum with three pairs long, tapering tubercles and two pairs rudimentary (Fig. 10E), the anterior pair of long tubercles with short setae at apex. Prothoracic horn (Fig. 10F) knob-like, smooth, with short stem and bearing 20.5 (17-23) and 22.33 (17-29) spiracular papillae in female and male respectively in a row curving along posterior side; horn length to width 2.14 ± 0.19: 1 in female and 2.30 ± 0.13: 1 in male; tracheal length about equal to horn length in both sexes, 1.00 ± 0.03 in female and 0.98 ± 0.03 in male.

Abdominal segments 1-4 with two pairs of tubercles on dorsum, posterior pair setigerous, setae directed posteriorly; segments 5-7 with single pair of setigerous tubercles, setae directed anteriorly, and with a median pair of faint cuticular markings, suggesting rudimentary tubercles; segment 8 with single medial and paired dorsolateral cuticular markings and segment 9 with paired tubercles, at extremity just anterior to base of terminal processes, which are closely approximated in male and wider apart in female. Male sexual processes dorsal, short. Terminal processes with length, width, and depth in proportion of 2.19 ± 0.75: 1 : 1.02 ± 0.35 in female and 3.33 ± 0.23: 1 : 1.07 ± 0.09 in male.

Cuticular armature finely shagreened.

Adult Female.-

Length 2.12 ± 0.14 mm. Wing (Fig. 11C) 1.07 ± 0.08 mm. by 0.47 ± 0.04 mm.

Head with mouthparts and antennae brown; eyes dark, contiguous. Maxillary palp (Fig. 11B) stout, with third segment bearing large, deep, conical sensory pit at proximal third of segment; PR 2.45 ± 0.12. Antenna (Fig. 11A) with segments 3-9 pyriform and segments 10-14 tapering; AR 0.74 ± 0.02.

Thorax brown with mesonotum and scutellum (Fig. 11F) shining and bearing numerous long erect dark bristles and short suberect yellowish hairs. Postscutellum and pleura shining brown; humeri and region around and ventral to wing base yellow. Legs brown with knee, basal half of femur and tip of tibia yellowish; mid and hind tibiae with row of lanceolate brown scales on hind margin; TR 1.45 ± 0.05 in fore leg, 1.17 ± 0.08 in middle leg and 1.11 ± 0.05 in hind leg; apical tibial comb with 8.2 (8-9) bristles.

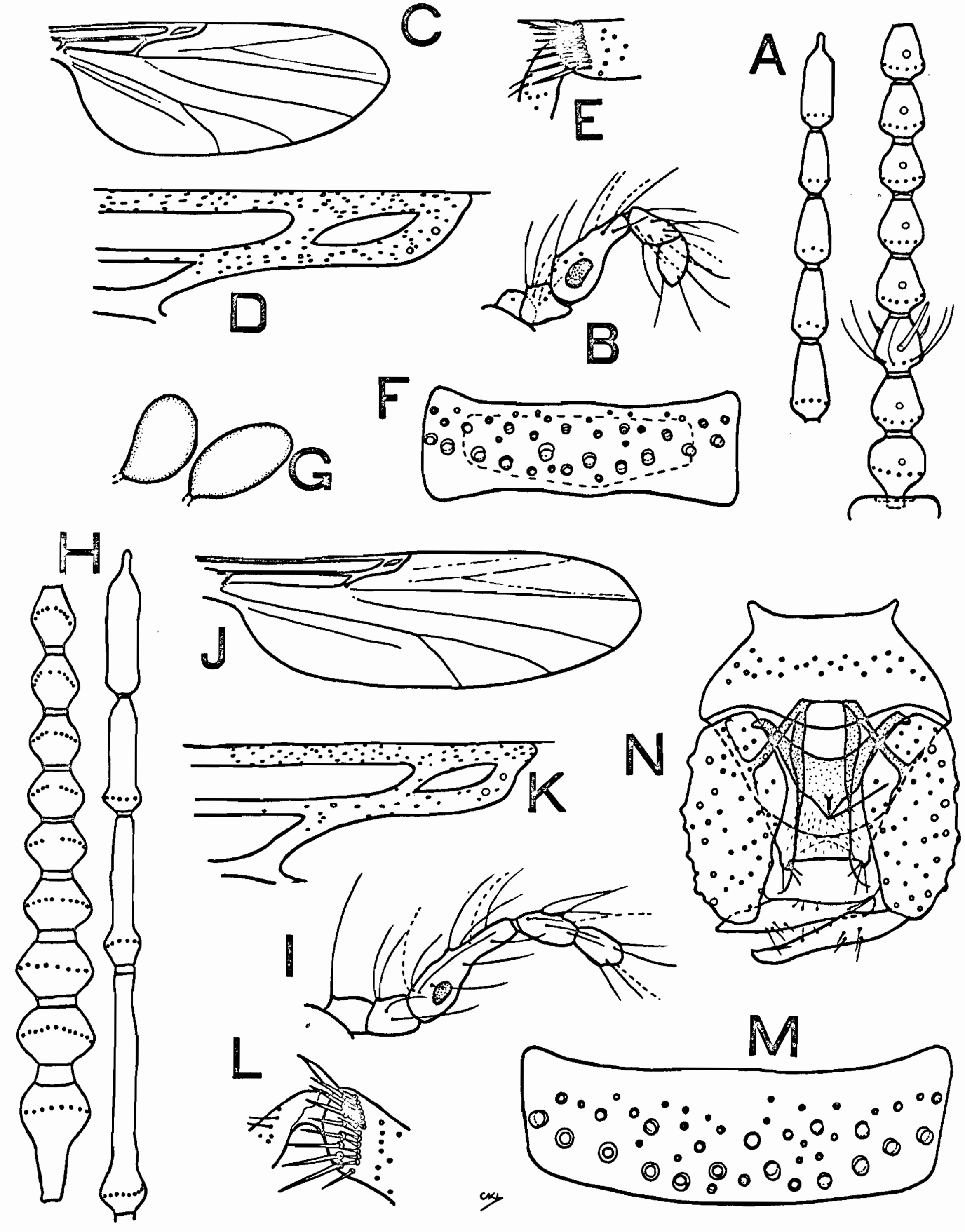
Wings brown, with veins darker brown, very densely covered with long, brown macrotrichiae; two prominent yellow costal spots, covered with yellow hairs, one at wing base before humeral vein, and the other covering end of second radial cell; CR 0.44 ± 0.02. Venation: vLR 1.16 ± 0.02: 1 : 1.87 ± 0.12; rs/r_1 1.54 ± 0.08; first radial cell completely obliterated, second radial cell narrow, elliptical, about as long as first (1.02 ± 0.19: 1) (Fig. 11D); m_{3+4} about twice length

Fig. 11. Forcipomyia (Forcipomyia) bipunctatapropinqua n. sp.

A-G, Adult female:
- A, Antenna
- B, Maxillary palp
- C, Wing
- D, Anterior wing venation
- E, Hind tibial comb
- F, Scutellum
- G, Spermathecae

H-N, Adult male:
- H, Antenna
- I, Maxillary palp
- J, Wing
- K, Anterior wing venation
- L, Hind tibial comb
- M, Scutellum
- N, Genitalia

Fig. 11



of cu_1 (1.90 ± 0.15: 1); fmcu under about middle of second radial cell (Fig. 11C). Halteres yellowish white with stems slightly infuscated.

Abdomen brown, covered with brown hairs; cerci and middle of ventral sclerites yellow, pleura of first abdominal segment also yellow. Spermathecae (Fig. 11G) two, oval, subequal, measuring 73.83 ± 8.16 μ x 44.51 ± 3.43 μ and 80.04 ± 7.46 μ x 44.51 ± 2.12 μ.

Adult Male.-

Length 2.46 ± 0.21 mm. Wing (Fig. 11 J) 1.18 ± 0.06 x 0.41 ± 0.03 mm. Color as in female.

Head brown. Antenna (Fig. 11H) with dark brown hairs, plume reaching to end of segment 13; AR 1.10 ± 0.07. Maxillary palp (Fig. 11I) slender with segment 3 bearing shallow, small sensory pit at basal third; PR 3.32 ± 0.15.

Thorax with scutellum bearing bristles as shown (Fig. 11M). Legs brown, with only knees and tips of tibia yellowish; TR 1.29 ± 0.03 in fore leg, 1.01 ± 0.05 in middle leg and 1.00 ± 0.05 in hind leg; apical tibial comb (Fig. 11L) with 9.1 (9-10) bristles.

Wings as in female; CR 0.43 ± 0.01. Venation: vLR 1.11 ± 0.04: 1: 1.82 ± 0.07; rs/r_1 1.63 ± 0.12; first radial cell obliterated, second radial cell elliptical, about as long as first (0.95 ± 0.10: 1) (Fig. 11K); fmcu under about tip of costa. (Fig. 11J).

Abdomen with dorsal and ventral sclerites brown and pleura yellowish white; dorsal scleritics with thin median longitudinal streak of whitish yellow running from first segment to about seventh where it disappears; two longitudinal yellowish-white bands running on ventral sclerites of segments 1-5.

Genitalia (Fig. 11N): sternite 9 about half as long as wide (0.46 ± 0.03: 1), tergite 9 also about half as long as wide (0.48 ± 0.07: 1). Parameres with basimeres broad basally, gradually tapering to narrow distal end, about twice as long as wide (2.21 ± 0.07: 1), and telomeres 5½ times as long as wide (5.47 ± 0.31: 1); telomeres slender with curved tips and about 0.8 times as long as basimeres (0.81 ± 0.03: 1). Aedeagus shield-shaped, about 0.7 times as long as width at base (0.67 ± 0.13: 1); basal arch very shallow; apex bipartite, parts closely approximated and appearing as bluntly pointed, tip bearing a filamentous long process which is easily broken off. Claspettes widely separated at base, basal union a narrow sclerotized band, claspette processes broad at anterior half and filiform at posterior half, reaching to beyond ends of cerci and before ends of basimeres.

Holotype (fourth instar larva): Collected in June 1963 under dry cowdung heaps at Morgan Arboretum, Macdonald College, Quebec, Canada. Deposited in Lyman Entomological Museum, Macdonald College.

Paratypes: Collected from the same habitat. Many larvae, pupae, males and females, associated pupal exuviae in personal collections.

This species is very close to bipunctata (Linnaeus) (1767) but differs from the latter in that the larva possesses on its anal pseudopod four hooks on either side of the median line without the additional pair of "small hooks in the middle", all these hooks being directed forward and not backward as described by Saunders (1924). The larva is also different from that of bipunctata in having three weak central hooklets on each branch of the bifid prothoracic pseudopod instead of just "two weak central ones" as described by Saunders (1924). The genitalia are also different in that they have a long filamentous process at the apex of the aedeagus, which, however, is easily broken.

Forcipomyia (Forcipomyia) intonsa CHAN NEW SPECIES

Larva.-

Length of third instar larva 2.61 mm. Color in life pale brown with head and setae of dark brown.

Head with chaetotaxy as shown (Fig. 12A); setae p, q, s, t and u spiny. HR 1.54; AR 2.53; qt/ts/sq in proportion of 1.38: 1.71: 1; tt/ant 0.45; qq/eyes 0.28; qq/ss 0.27.

Prothorax bears a pair of typical hygroscopic spear-shaped a setae and six other pairs of setae; b and d setaes joined at base; setae b, c and d spiny and stout; e and f smooth, long; h (?) setae paired, minute and one minute pair of setae on one side of prothoracic pseudopod. Prothoracic pseudopod (Fig. 12D) divided medially at about 2/3 its length from base, each lobe bearing on inner side five hooklets; length, width and depth in proportion of 1.58: 0.86: 1. Meso- and meta-thorax basically similar in chaetotaxy to prothorax, with eight pairs of setae, one minute pair with paired setae.

Abdominal segments 1-7 similar in chaetotaxy, with nine pairs of setae (Fig. 12C); segments 8 and 9 with chaetotaxy as shown (Fig. 12B). Posterior pseudopod (Fig. 12E) with transverse ridge bearing two rows of hooks, anterior row with eight hooks and posterior row with 10 hooks.

Cuticular armature comprised of minute spines (Figs. 12, B,C).

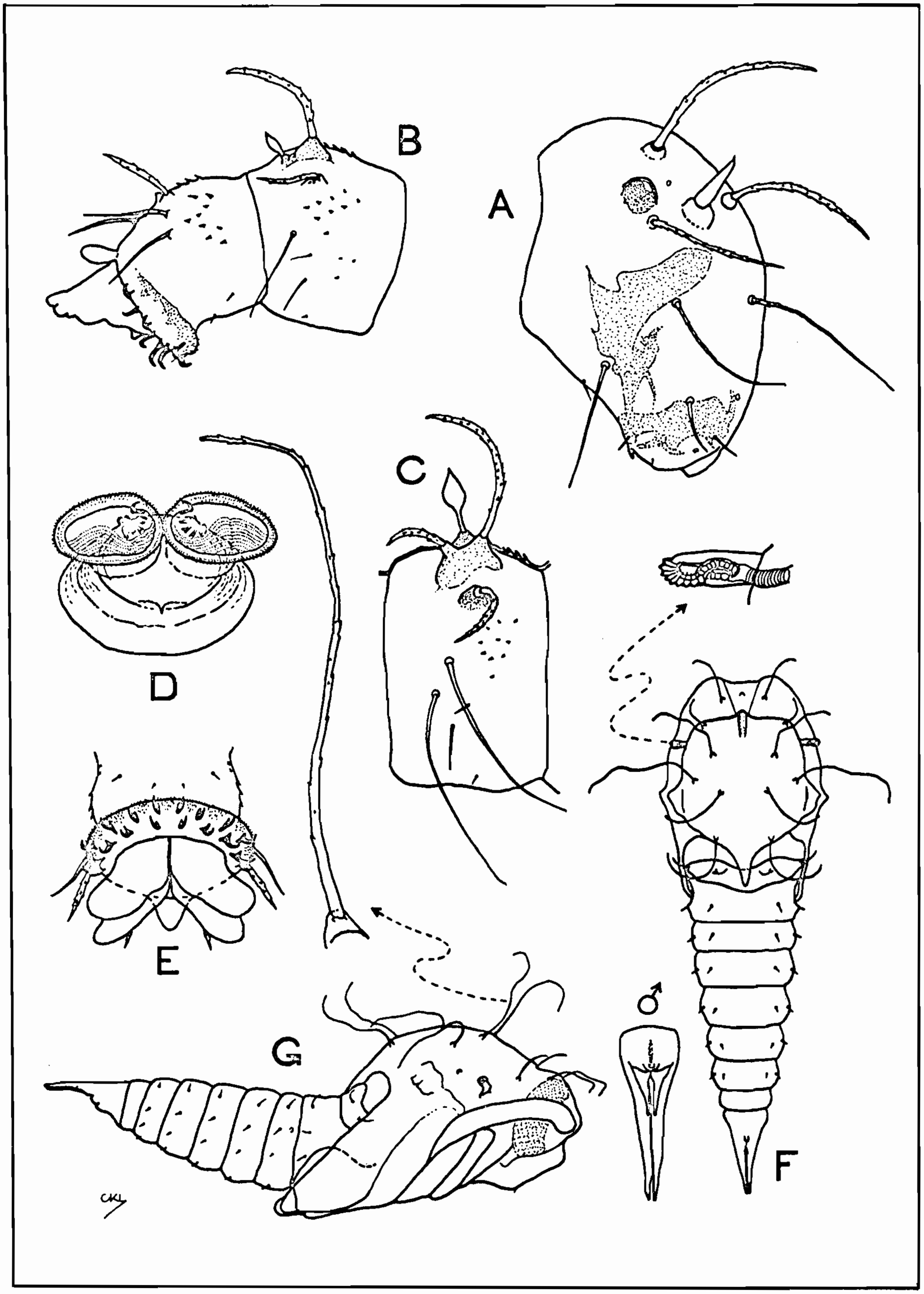
Pupa .-

Length 3.06 mm. in female and 3.03 mm. in male. Color pale orange,

Fig. 12. _Forcipomyia_ (_Forcipomyia_) _intonsa_ n. sp.

- A-E, Third-instar larva:
  - A, Head
  - B, Last two segments
  - C, Third abdominal segment
  - D, Prothoracic pseudopod
  - E, Anal pseudopod
- F-G, Pupa:
  - F, Pupa, dorsal view
  - G, Pupa, lateral view

Fig. 12



darker orange on thorax, and dark just prior to adult emergence.

Median head sclerite with a small median tubercle; lateral sclerites each with a setate tubercle, the antero-dorsal tubercle. On the postero-ventral region of each side of the head near the mid-line is a pair of minute setae, the ventro-median tubercles; the ventro-lateral tubercles are absent. Cephalothorax 2.02 times its greatest width in female and 1.96 in male. Ratio of length of head to thorax 0.34 in ventral aspect and 0.20 in dorsal aspect in female and respectively 0.35 and 0.22 in male.

Thorax bearing five pairs of tubercles with elongate setae (Fig. 12F,G) and a median ridge (Fig. 12F). Prothoracic horn small, club-shaped, bearing 18-22 spiracular papillae curving up back and over top in an S-shape, 2.31 times as long as greatest width in female and 2.56 in male; tracheal length in horn to horn length 0.83: 1 in female and 0.85: 1 in male.

Abdominal segments 1-7 with two pairs of tubercles on dorum, the dorso-median and the dorso-lateral (Fig. 12F). Segment 2 has, in addition, a pair of ventro-lateral tubercles (Fig. 12G) and segments 3-7 have, in addition, to the ventro-lateral, a pair of ventro-median tubercles (Fig. 12G). Segments 8 and 9 do not bear tubercles. Terminal processes of last segment in both sexes elongate and tapering to pointed tip, those of the male longer than those of the female; length, width and depth in proportion of 4.20: 1: 1.44 in female and 5.12: 1: 1.23 in male. Similar ratios for third abdominal segment 1: 1.84: 1.74 in female and 1: 1.86: 1.76 in male. Sexual processes in male dorsal, small; length, width and depth in proportion of 3.25: 1.00: 1.

Pupa retaining larval exuviae in last six abdominal segments.

Adult Female.-

Length 2.45 mm. Wing 1.40 x 0.56 mm.

Head and mouthparts uniformly dark brown; clypeus (Fig. 13C) with seven setae. Maxillary palp (Fig. 13B) long, with segment 3 large, swollen, narrowed at apical quarter and bearing a deep sensory pore with small opening; five segments in proportion of 12: 19.5: 39: 21.5: 10; PR 3.11. Antenna (Fig. 13A) with scape and pedicel dark brown, basal flagellar segments short; segment 2-9 yellow brown and apical five segments brown; AR 1.52; segments 2-14 in proportion of 15: 11;11.5: 11.5: 11.5: 11.5: 11.5: 13: 28: 30: 28: 28.5: 36; segments 2-5 somewhat globular, as wide as long; segments 6-9 slightly longer than wide.

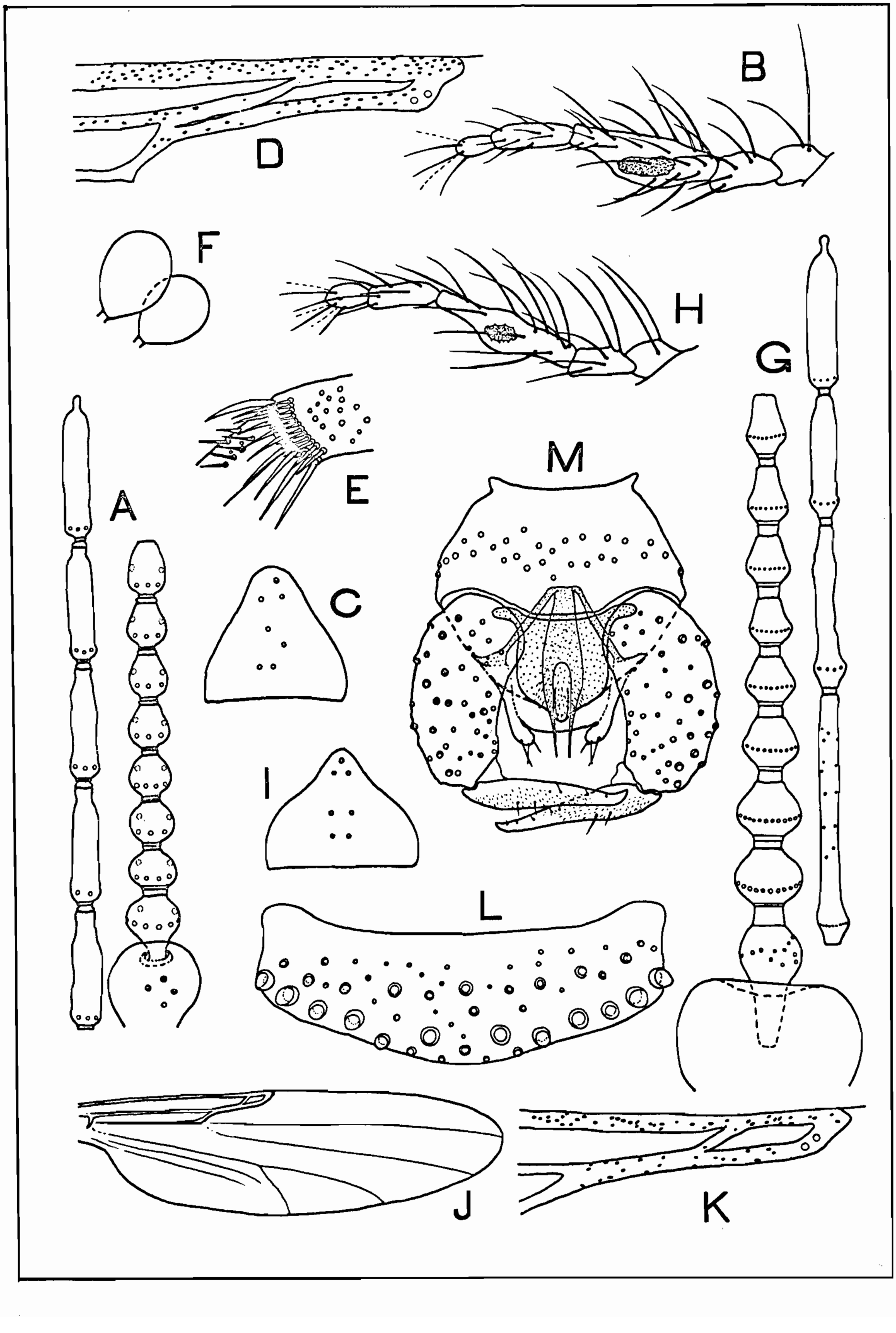
Thorax uniformly dark brown; scutellum with 13 strong bristles. Legs with narrow scales on entire length, mainly yellow brown, with dark brown bands at distal and proximal ends of femur and tibia respectively on both middle and hind legs, occupying about distal half of femur and proximal one-eighth of tibia of middle; claws slender, empodia thick; TR 0.70 in fore leg, 0.44 in middle and 0.52 in hind leg; leg segments except for basal two in proportion of 110: 125: 38: 54: 27: 21.5: 17 in fore leg, 133: 160: 61: 30: 24: 18 in middle, and 144: 152: 35.5: 68: 34: 27: 19 in hind leg.

Wing brown, costa and radius darker brown, with black scales and hairs. CR 0.54. Venation: rs/r_1 2.08; first radial cell slit-like, almost obliterated, second radial cell rather long, narrow, longer than first (1.91: 1); fmcu just under end of first radial cell; m_{3+4}/cu_1 2.00. Halteres yellow.

Fig. 13. Forcipomyia (Forcipomyia) intonsa n. sp.

A-F, Adult female:
  A, Antenna
  B, Maxillary palp
  C, Clypeus
  D, Anterior wing venation
  E, Hind tibial comb
  F, Spermathecae
G-M, Adult male:
  G, Antenna
  H, Maxillary palp
  I, Clypeus
  J, Wing
  K, Anterior wing venation
  L, Scutellum
  M, Genitalia

Fig. 13



Abdomen dark brown; tergites and pleural membranes with dark brown, narrow scales, sternites with dark brown hairs and narrow scales; cerci yellow brown. Spermathecae two, oval, subequal, brown, 79.31 x 55.17 μ and 72.41 x 55.17 μ, with narrow necks and short sclerotized ducts.

Adult Male.-

Length 2.59 mm. Wings 1.42 x 0.44 mm.

Head including mouthparts dark brown; clypeus (Fig. 13I) with seven setae; proboscis about as long as head capsule (0.95: 1), Maxillary palp (Fig. 13H) rather slender, segment 3 swollen in middle and bearing deep sensory pore with very small opening, length of segments in proportion of 8: 15: 29: 13: 10; PR 3.89. Antenna (Fig. 13G) with pedicel dark brown, other segments including plume lighter brown; segments 2-14 in proportion of 25: 14: 14: 14: 14: 13.5: 13.5: 14: 16: 52: 34: 29: 32; AR 1.19.

Thorax uniformly brown; scutellum (Fig. 13L) with 12 strong bristles in posterior row. Legs with coloration generally similar to those of female but middle femoral preapical dark brown bands smaller, and middle and hind tibiae with sub-basal, small brown bands, sometimes obscure; claws large, slender, and strongly curved; empodia moderately large; TR 0.56 in fore leg, 0.34 in middle leg and 0.40 in hind leg.

Wings brown with grey hairs. CR 0.47-0.54. Venation: vLR 1.09: 1: 1.56; rs/r_1 1.48; first radial cell obliterated, second radial cell small, rather wide, shorter than first (0.69: 1); fmcu under about middle of second radial cell; m_{3+4}/cu_1 2.42. Halteres pale brown.

Abdomen dark brown, with intersegmental yellow bands and basal tergites with median broad yellow stripe and bearing narrow scales. Genitalia (Fig. 13M) entirely dark brown; sternite 9 0.46 times as long as its greatest width, tergite 9 0.54 times as long as its width.

Parameres with basimeres short and wide, about twice as long as wide (2.09: 1), and telomeres boat-shaped, curved at pointed tip, gradually tapering from broad base to tip, 5.43 times as long as greatest width. Telomeres shorter than basimeres (0.84: 1). Aedeagus shield-shaped, longer than wide (1.15: 1), mesal point bluntly pointed, basal arms rather slender, produced laterally. Claspettes rather widely separated at base, with basal union short, extending and connecting posteriorly with claspette processes which are about as long as their common union from the basal union and which reach to slightly beyond tip of cerci.

Holotype (pupa).- Collected from mosses, liverworts and bluegreen algae on claybank at Wallace Way, Singapore in May 1962. Deposited in Lyman Entomological Museum, Macdonald College, Quebec.

Paratypes.- Collected from same locality and habitat as holotype; 17 larvae, 4 females, 9 males and 14 associated pupal exuviae in personal collections.

This species is distinct from all other species described in the very long thoracic processes of the pupa. The male genitalia are typical of the subgenus, thus offering no really good taxonomic character. They resemble closest those of *esakiana* Tokunaga (1940) and *flavitibialis* Tokunaga and Murachi (1959), among a host of other species with similar types of claspettes and aedeagus. It however differs from *esakiana* in the larger palpal ratio of the female (3.1 against 2.0) and in other minor characters. In the male, its hind TR is smaller than that of *esakiana* (0.40 to 0.44).

It also differs from *flavitibialis*, in the female, in the narrower third palpal segment and in the much longer fourth, and in the smaller AR (1.52 to 1.83), and in the male, in the smaller hind TR (0.40 to 0.47), the slightly curved basal arms of the aedeagus and the straight tips of the claspette processes. In *flavitibialis* the basal arms of the aedeagus are straight and the tips of the claspette processes slightly outward-turning.

Forcipomyia (*Forcipomyia*) *swezeyanaadfinis* CHAN NEW SPECIES

Larva.-

Length of full-grown fourth instar larva 2.58 mm. Color whitish with gut contents dark.

Head brown; eyes, antennae and setae as figured (Fig. 14B). HR 1.84; AR 2.17; pq/qs/sp 1.46: 0.71: 1; tt/ant 0.57; qq/eyes 0.27; qq/ss 0.23.

Prothoracic *a* and *b* setae with filament and tubercle in proportion of 10.8 and 9.8 respectively; prothoracic pseudopod bifid, with length, width and depth in proportion of 1.67: 1.33: 1 and bearing on apex of each branch six black hooks.

Chaetotaxy on abdominal segments 1-7 similar (Fig. 14D), that on segments 8 and 9 as figured (Figs. 14A, 14E). Anal pseudopod (Fig. 14E) armed with two rows of four hooks each on either side of median line; anal blood gills two, each unequally bilobed.

Cuticular armature confined to dorsum (Fig. 14D), consisting of minute, scales; ventral integument smooth.

In full-grown larva near pupation, abdominal segments 1-8 develop a transverse cuticular bar connecting the bases of the *a* hairs.

Pupa (Male).-

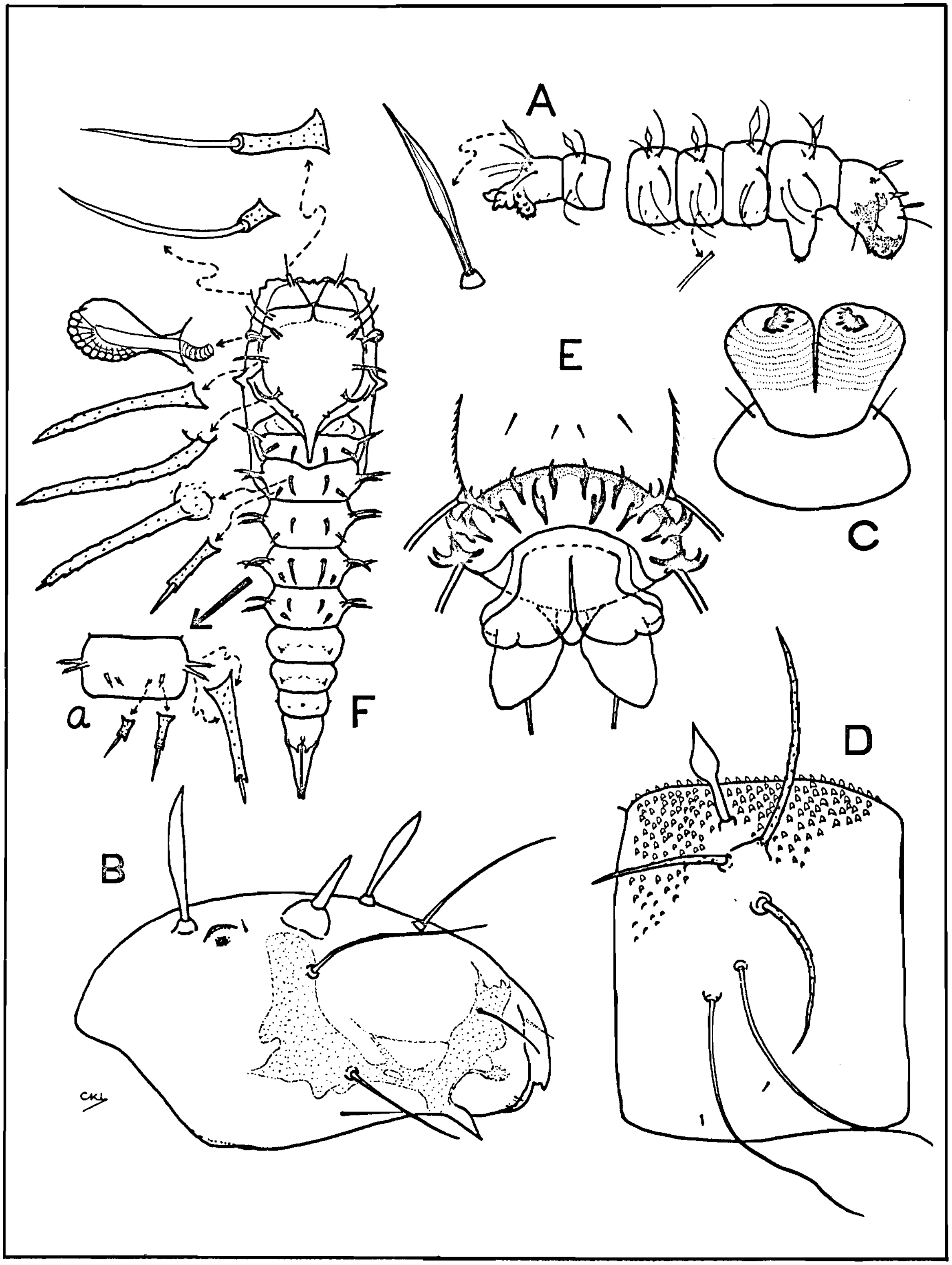
Length 2.40-2.45 mm. Color as in larva but dark just prior to

Fig. 14. _Forcipomyia_ (_Forcipomyia_) _swezeyanaadfinis_ n. sp.

A-E, Fourth-instar larva:
  - A, Larva, lateral view
  - B, Head
  - C, Prothoracic pseudopod
  - D, Third abdominal segment
  - E, Anal pseudopod

F, Pupa: Dorsal view

Fig. 14



emergence of adult. Larval exuviae retained in last segments.

Median head sclerite with low tubercle and lateral sclerites each with an elongate tubercle (Fig. 14F). Cephalothorax 1.80-1.97 times longer than its greatest width. Ratio of head to thorax 0.21 in dorsal aspect and 0.37 in ventral aspect.

Thorax with five pairs of tubercles on dorsum (Fig. 14F), anterior two pairs bearing long seta on short tubercle, last pair rudimentary and third and fourth pairs elongate, without setae. Prothoracic horn club-shaped, twice as long as wide (1.92-2.00: 1), and bearing about 12 spiracular papillae along posterior edge.

Abdominal segments 2-5 and 6 and 7 with similar chaetotaxy arrangement on dorsum (Fig. 14F); segment 8 with three cuticular markings, only on dorsum, without tubercles. Segments 3-8 each with two pairs of tubercles on ventral surface. Terminal processes closely approximated, with length, width and depth in proportion of 4.22: 1: 1.22; sexual processes in male dorsal, short and similar ratios in proportion of 1.22: 1.72: 1.

Cuticular armature finely shagreened, composed of short, minute setae.

Adult Female.-

Length 1.70 mm. Wing (Fig. 15C) 0.79 x 0.35 mm. Color brown with head and thorax darker brown.

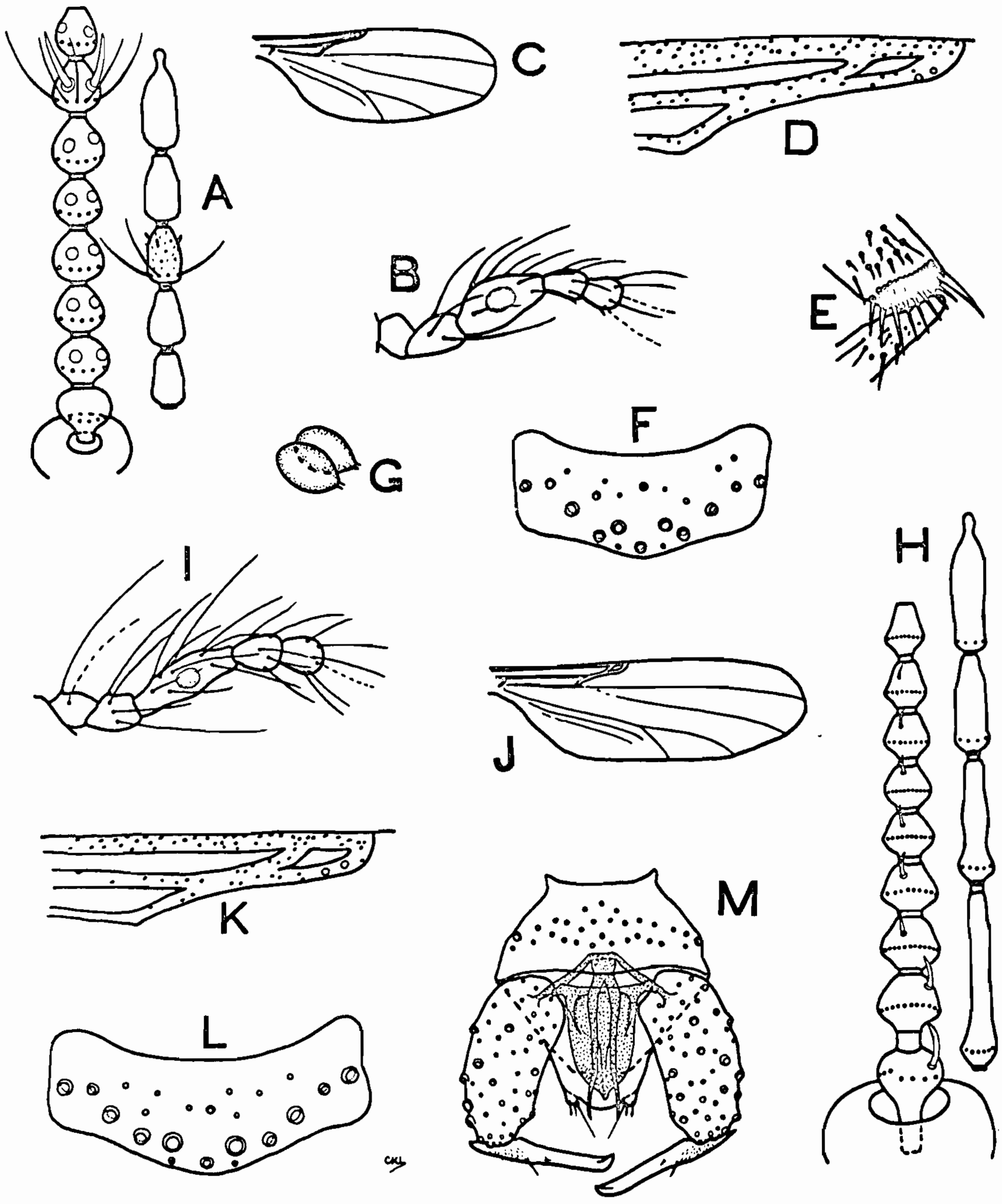
Head with antenna and mouthparts brown; eyes black, contiguous. Maxillary palp (Fig. 15B) short, with third segment bearing large, moderately deep sensory pit in middle; PR 1.90. Antenna (Fig. 15A) with segments 2-9 pyriform and segments 10-14 gradually elongating, last segment longest; AR 0.82.

Fig. 15. _Forcipomyia_ (_Forcipomyia_) _swezeyanaadfinis_ n. sp.

A-G, Adult female:
  - A, Antenna
  - B, Maxillary palp
  - C, Wing
  - D, Anterior wing venation
  - E, Hind tibial comb
  - F, Scutellum
  - G, Spermathecae

H-M, Adult male:
  - H, Antenna
  - I, Maxillary palp
  - J, Wing
  - K, Anterior wing venation
  - L, Scutellum
  - M, Genitalia

Fig. 15



Thorax brown with scutellum darker brown and bearing setae as arranged in Fig. 15F. Legs brown, with base of femur, femo-tibial joints of all legs and distal end of tibia of hind leg pale; fore TR 1.35, mid TR 0.92, hind TR 0.90; apical tibial comb with eight bristles.

Wings brown, covered densely with brown hairs. CR 0.42. Venation: vLR in proportion of 1.20: 1: 2.00; rs/r_1 1.55; first radial cell obliterated, second radial cell narrow, shorter than first (0.65: 1) (Fig. 15D); fmcu ending just under before tip of costa; m_{3+4}/cu_1 1.98. Halteres brown.

Abdomen, including cerci, brown, covered with brown hairs. Spermathecae (Fig. 15G) two, subequal, with very narrow ducts, 48.3 x 31 μ, and 41.4 x 31.1 μ.

Adult Male.-

Length 1.88 mm. Wing (Fig. 15J) 0.90 x 0.45 mm. Color as in female.

Head brown, with antennae and mouthparts brown; eyes dark, contiguous. Antenna (Fig. 15H) with dark brown hairs; AR 1.02. Maxillary palp (Fig. 15I) slender, with third segment long and bearing large, shallow, sensory pit in middle; PR 2.80.

Thorax with scutellum bearing bristles as shown (Fig. 15L). Color of legs as in female; fore TR 1.19, mid TR 0.71, hind TR 0.67; apical tibial comb with eight bristles.

Wings with CR 0.41. Venation: vLR 1.18: 1: 2.00; rs/r_1 1.61; first radial cell obliterated, second radial cell small, rather narrow, about equal in length to first (0.93: 1) (Fig. 15K); fmcu under some distance beyond tip of costa.

Abdomen brown, broad basally and tapering to small genitalia.

Genitalia (Fig. 15M): sternite 9 about 0.4 times as long as wide (0.36: 1); tergite 9 two-fifths as long as wide (0.40: 1). Parameres with basimeres very slightly curved, about twice as long as wide (2.12: 1) and telomeres shorter than basimeres (0.83: 1), almost straight, curving at apex, and about six times as long as its greatest width at base (5.80: 1). Claspettes very widely separated basally, basal union short, with claspette processes reaching to beyond tip of cerci, b/c/b 2.83: 1: 2.83.

Holotype (fourth instar larva).- Collected between bark and wood of decaying tapioca (*Manihot utilissima* Pohl) stem, at Wallace Way, Singapore, 1962.

Paratypes.- Collected from same locality and habitat as holotype; 4 females, 30 males, 4 pupae and 33 pupal exuviae, in personal collections.

This species is very close to *Forcipomyia* (*Forcipomyia*) *swezeyana* Tokunaga & Murachi (1959), but differs from the latter in the following points: (i) the *b* setae of the larva are not joined to the *d* setae, (ii) the larval anterior pseudopod bears six hooklets instead of 16 on each of the bifid branches, (iii) pupal abdominal segments with four pairs, instead of five, of large tubercles, (iv) the male genitalia with distinct basal union instead of an indistinct one, (v) the basimeres are uniformly cylindrical and much narrower instead of broad basally and narrow distally and wide.

Forcipomyia (*Forcipomyia*) *securis* CHAN NEW SPECIES

Larva.-

Length of full-grown fourth instar 3.44 mm. Color pale yellow with gut contents brown.

Head light brown, with mouthparts dark; eyes, antennae and setae as in Fig. 16B. p and q setae lanceolate, others simple; HR 1.76; AR 3.10; qt/ts/sq in proportion of 1.61: 2.00: 1; tt/ant 0.44; qq/eyes 0.26; qq/ss 0.25.

Prothoracic a setae sword-shaped, b setae simple, curved, with anterior side fringed; prothoracic pseudopod bifid from about middle to apex and bearing on apex of each branch eight (5 stronger, curved, and 3 weaker, less curved) black hooks (Fig. 16C).

Chaetotaxy on abdominal segments 1-7 similar (Fig. 16A), that on segment 8 and 9 as figured (Fig. 16A). Anal pseudopod (Fig. 16D) armed with two rows of four curved hooks each on either side of median line; anal blood gills two, bilobed; cauda short, bluntly pointed.

Cuticular armature confined to dorsum, scale-like; ventral integument smooth.

In full-grown fourth instar near pupation, abdominal segments 1-8 bear a transverse cuticular bar connecting the bases of the a hairs.

Pupa.-

Length 2.48mm. in male and 2.40 mm. in female. Color as in larva but dark just prior to emergence of adult. Exuviae ochreous, with prothoracic horn brown. Larval exuviae retained in last four segments.

Head sclerites without tubercles. Cephalothorax 1.53 times longer than its greatest width in female and 1.70 in male. Ratio of head length to thorax length 0.44 in ventral aspect and 0.20 in dorsal aspect in female and respectively 0.45 and 0.20 in male.

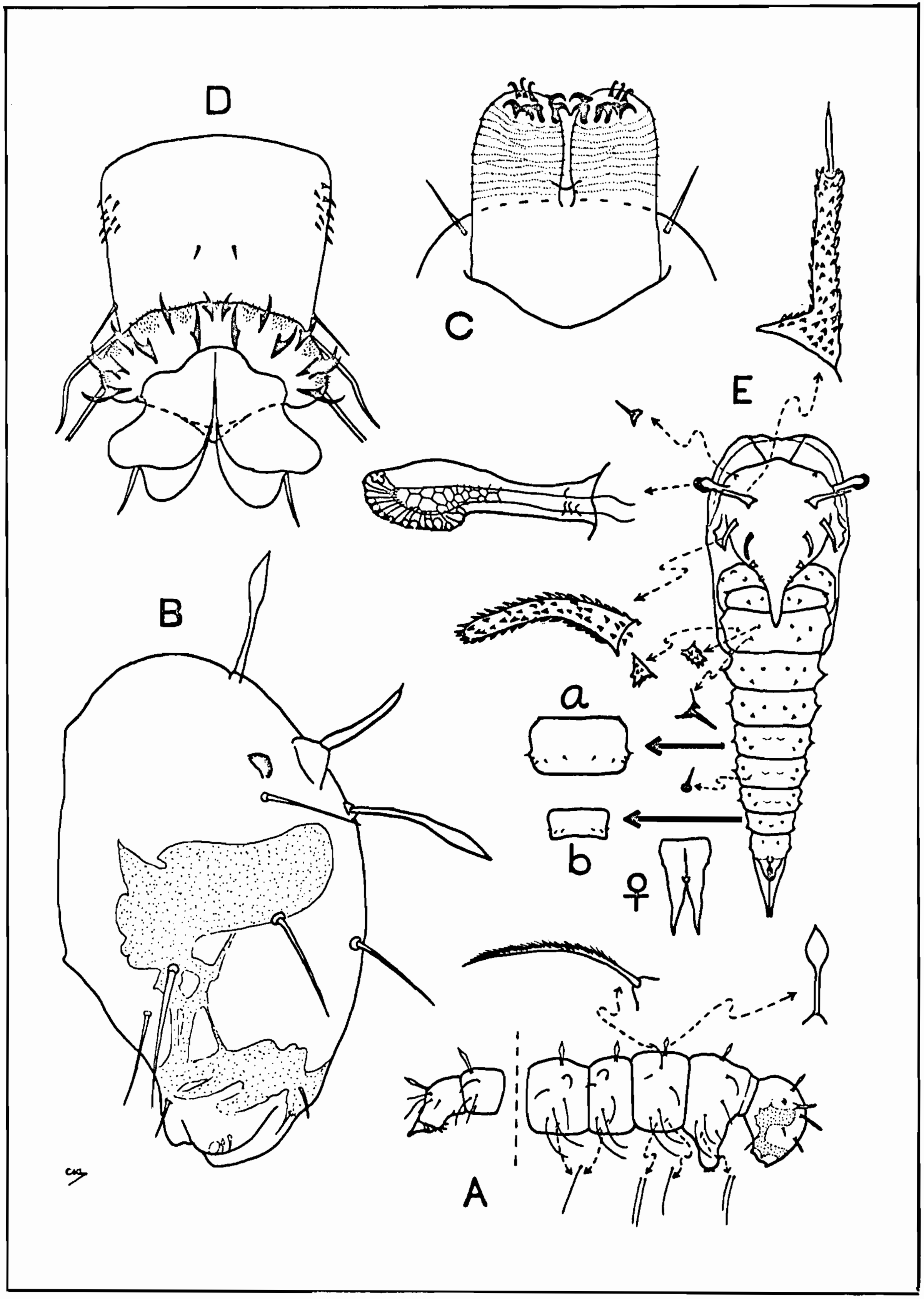
Thorax with six pairs of tubercles on dorsum (Fig. 16E), anterior

Fig. 16. Forcipomyia (Forcipomyia) securis n. sp.

- A-D, Fourth-instar larva:
  - A, Larva, lateral view
  - B, Head
  - C, Prothoracic pseudopod
  - D, Anal pseudopod

- E, Pupa: dorsal view
  - a, Fifth abdominal segment, ventral view
  - b, Eigth abdominal segment, ventral view

Fig. 16



two pairs setigerous. Prothoracic horn axe-shaped, about three times as long as wide (3.13: 1 in female and 3.63: 1 in male), and bearing 17-18 spiracular papillae along curved posterior edge.

Abdominal segments 1-4 with three pairs of tubercles on dorsum (Fig. 16E); segments 5-7 with two pairs of tubercles on dorsum and a median pair of cuticular markings; segments 3-7 similar in chaetotaxy ventrally, with three pairs of minute lateral setae and one pair of minute latero-ventral and one pair of minute ventral tubercles (Fig. 16E, a); segment 8 similar to segments 3-7 but with only one pair lateral tubercles (Fig. 16E, b). Terminal processes closely approximated in male, divergent in female, with length, width and depth in proportion of 1.92: 2.16: 1 in female and 3.33: 0.92: 1 in male. Male sexual processes dorsal, short, with length, width and depth in proportion of 1.04: 1.18: 1.

Cuticular armature finely shagreened, composed of short, minute setae.

Adult Female.-

Length 1.49 mm. Wing (Fig. 17B) 0.81 x 0.36 mm. Color brown.

Head with eyes dark and antennae and mouthparts brown. Maxillary palp (Fig. 17D) rather slender, with segment 3 long and bearing shallow sensory pit in middle of basal third portion; PR 2.33. Antenna (Fig. 17A) with segments 2-9 flask-shaped and segments 10-13 longer, also flask-shaped and segment 14 distinctly longer than the rest; AR 0.51.

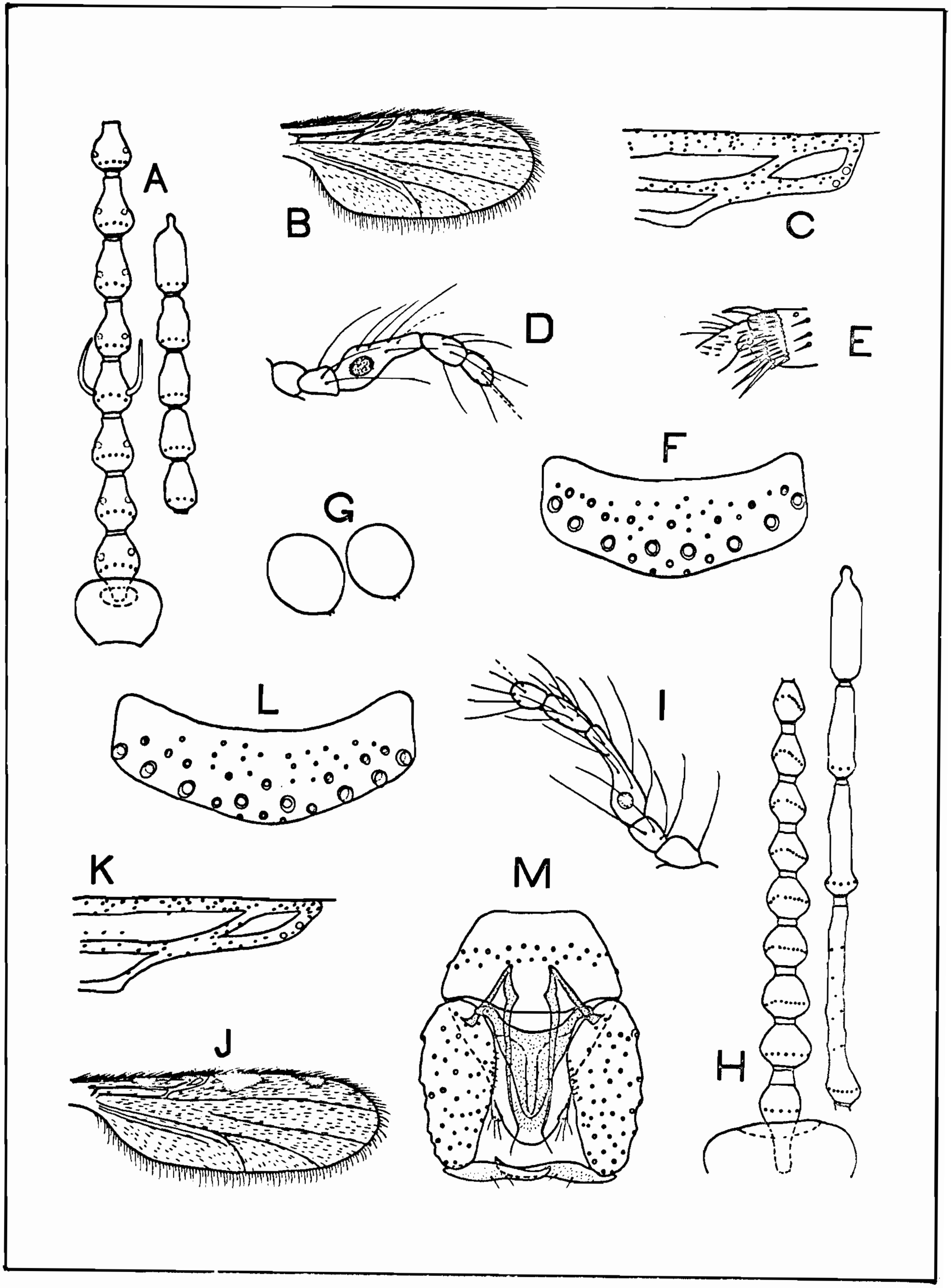
Thorax dark brown with scutellum bearing eight strong bristles in caudal margin (Fig. 17F). Legs pale brown, with TR of fore leg 1.13, middle leg 0.76 and hind leg 0.80; tibial comb with eight bristles.

Wings brown, covered with dense brown hairs; CR 0.41. Venation: vLR 1.22: 1: 2.33; rs/r_1 1.60; first radial cell obliterated, second radial cell short, rather wide, longer than first (1.26: 1) (Fig. 17C);

Fig. 17. _Forcipomyia_ (_Forcipomyia_) _securis_ n. sp.

A-G, Adult female:
  A, Antenna
  B, Wing
  C, Anterior wing venation
  D, Maxillary palp
  E, Hind tibial comb
  F, Scutellum
  G, Spermathecae
H-M, Adult male:
  H, Antenna
  I, Maxillary palp
  J, Wing
  K, Anterior venation of wing
  L, Scutellum.
  M, Genitalia

Fig. 17



m_{3+4}/cu_1 1.95; fmcu under about end of costa.

Abdomen brown, covered with brown hairs. Spermathecae (Fig. 17G) two, subequal, without necks, with very narrow ducts, and measuring 69 x 58.65 μ and 62.1 x 55.2 μ.

Adult Male.-

Length 1.77 mm. Wing (Fig. 17J) 0.98 mm. by 0.33 mm. Color brown.

Head with eyes dark, pedicels dark brown and antennae and mouthparts lighter brown. Antenna (Fig. 17H) with plume brown, AR 1.16. Maxillary palp (Fig. 17I) long, slender, with third segment long and bearing small sensory pit in middle of swollen basal third portion; PR 3.13.

Thorax dark brown, with scutellum bearing eight strong bristles (Fig. 17L). Legs pale brown, tibiae bearing long hairs; TR 1.00 in fore leg, 0.63 in middle leg and 0.70 in hind leg; apical tibial comb bearing nine bristles.

Wings brown, densely covered with brown hairs and bearing three black spots as shown in Fig. 17J; CR 0.40. Venation: vLR 1.10: 1: 1.90; rs/r_1 1.46; first radial cell obliterated, second radial cell small, moderately wide, longer than first (1.29: 1) (Fig. 17K); fmcu under slightly beyond end of costa; m_{3+4}/cu_1 2.32.

Abdomen pale brown. Genitalia (Fig. 17M): sternite 9 about half as long as wide (0.51: 1); tergite 9 about three-quarters as long as wide (0.77: 1). Parameres with basimeres long, about $2\frac{1}{2}$ times as long as width at base (2.56: 1), gradually tapering from base to tip; telomeres curved inwards at middle and at distal end, shorter than basimeres (0.68: 1) and about six times as long as width at base (6.22: 1).

Aedeagus shield-shaped, with mesal point bluntly pointed and basal arms curving backwards at distal ends. Claspettes widely separated at base and bearing at ends backward-directed claspette processes reaching to about end of basimeres.

Holotype (pupa).- Collected from decaying wood at base of a fallen rotting fig tree at Wallace Way, Singapore in 1962. Deposited in the Lyman Entomological Museum, Macdonald College, Quebec, Canada.

Paratypes.- Collected from same habitat and locality as holotype; 11 larvae, 9 females, 12 males and 11 associated pupal exuviae, in personal collections.

This species, ins structure of male genitalia and in female hind TR, is close to Forcipomyia (Forcipomyia) mira Johannsen (1932) from Java. Johannsen's (1932) original description of mira is insufficiently quantitative to make adequate comparisons between the two species. However, this species differs from mira in the much smaller AR of the female (0.51 against 1.14), and in the narrower aedeagus in the male. The male genitalia also differ from those of mira in that the claspette processes have outward-turning tips instead of straight ones and the basimeres are broad basally, tapering to narrow distal ends instead of roughly uniformly cylindrical, and the telomeres are curved apically instead of roughly straight.

Since larval habitat is often very specific, the presence of mira larvae in tree sap and those of this species in decaying wood, furnishes an ecological distinction between the two species.

Other Species.-

This subgenus is very widespread and contains the great majority of the Forcipomyiinae. Although a considerable number of species descriptions attributable to this subgenus are found in the literature, only those species from which immature stages have been described are listed here. These include:

bipunctata Linnaeus (1767); Syst. Nat., 12th ed., 2: 978;
Wirth (1952), Univ.Calif. Publ.
Entomol. 9: 134

braueri Wasmann (1893); Wien. Ent. Zeitg. 12: 277;
Saunders (1924), Parasitology 16: 203

brevipennis Macquart (1826) Rec. Soc.Sci.Agr. Lille, p.179
Wirth (1952), Univ.Calif. Publ. Entomol.
9: 131

ciliata Winnertz (1852); Linn. Ent. 6: 1-80; Saunders (1924),
Parasitology 16: 200

cinctipes Coquillet (1905); Journ.N.Y. Entomol. Soc. 13: 64;
Wirth (1952), Univ. Calif. Publ. Entomol.
9: 128

corticis Kieffer (1911); Bull. Soc. Metz. 27: 1-60;
Saunders (1924), Parasitology 16: 205

nigra Winnertz (1852); Linn. Ent. 6: 1-80; Saunders (1924),
Parasitology 16: 197

picea Winnertz (1852); Linn. Ent. 6: 1-80; Saunders (1924),
Parasitology 16: 188

pulchrithorax Edwards (1924); Parasitology 16: 209; Saunders (1924),
Parasitology 16: 202

radicicola Edwards (1924); Parasitology 16: 208; Saunders (1924),
Parasitology 16: 195

raleighi Macfie (1938); Proc. Roy. Entomol. Soc. London 7: 160;
Saunders (1956), Can.J. Zool. 34: 660

squamipes Coquillet (1902); Proc. U.S. Nat. Mus. 25: 38;
Wirth (1952), Univ. Calif. Publ. Entomol.
9: 136

swezeyana Tokunaga and Murachi (1959); Insects of Micronesia
12(3): 145

texana Long (1902); Biol.Bull. 3: 10; Wirth (1952), Univ. Calif.
Publ. Entomol. 9: 138

4. SUBGENUS SCHIZOFORCIPOMYIA NEW SUBGENUS

Subgenus type lerouxi new species

I take great pleasure in naming this type species after Dr. E. J. Leroux.

Subgenus Schizoforcipomyia CHAN NEW SUBGENUS

Saunders (1956) has diagnosed larvae of Forcipomyia s. str. species as possessing anal pseudopods described as "a transverse ridge bearing two rows of hooklets; rarely divided into two lobes, each hook-crowned", but in none of his species has he described a larva with the latter condition, i.e. with a divided anal pseudopod and figured the male genitalia of such a species.

Larvae of a species having divided posterior pseudopod were collected under the bark of a rotten erect branch of an angsana tree. They resemble typical Forcipomyia s. str. larvae in most characters but differ in the presence of a secondary seta on the tubercle of the p hairs on the head, the absence of the s hairs, the longer, stouter b hairs of the body, and in the presence of four anal blood gills instead of two. In the adult male the claspettes are arch-like, resembling those of Proforcipomyia and lacking the backwardly directed claspette processes of Forcipomyia s. str. species. The aedeagus is V-shaped, joined only at the tip which bears two hooklets, a structure not seen elsewhere in the Forcipomyia although remotely resembling similar modifications in some Lasiohelea species. The male genitalia of this species are thus widely different from those of the typical Forcipomyia s. str. and inclusion of this species in Forcipomyia s. str. is unjustifiable.

A new subgenus, Schizoforcipomyia ("schizo", Greek for "split" referring to the larval posterior pseudopod), is therefore erected to accommodate the new species.

Like Warmkea Saunders this subgenus apparently is a "young" offshoot from the parent stock of Forcipomyia.

Diagnosis

Larva.-

Large, about 3 mm. long when fully grown. Head large, hypognathous, profile smoothly rounded; p hairs with secondary seta on tubercle, s hairs absent; antennae as in Forcipomyia s. str. but filament longer and more pointed. Body chaetae many, fairly long; a hairs spear-shaped, not so rounded as in Forcipomyia s. str. but more like those of Proforcipomyia. Prothoracic pseudopod medially divided, each half again subdivided but unequally and indistinctly, the larger outer quarter bearing a crown of hooklets on apex. Anal pseudopod bilobed, each lobe bearing eight hooks. Anal blood gills four, outer pair unequally bilobed. Cauda small, bluntly conical.

Pupa.-

Length about 2.4 mm. Spiny with many tubercles, most bearing short seta at apex. Larval exuviae retained in last few segments. Prothoracic horns thumb-shaped, short, with about 11 spiracular papillae curving across apex and posterior margin. Male sexual processes small, dorsal, on last abdominal segment.

Female.-

Length about 1.5 mm. TR about 1.5 in fore leg, 0.8 in middle leg and 1.0 in hind leg. Palps relatively short but stout, third segment very broad, with very deep, flask-shaped sensorium, fourth and fifth segments distinct, fifth longer; PR about 2. Antennae with basal flagellar segments 2-9 longer than wide, bearing paired hyaline setae slightly shorter than respective segments; distal five flagellar segments except longest last segment about equal in length; AR about 1.0. Wings with CR about 0.6, first radial cell completely obliterated, second radial cell small, moderately wide, about 1½ times as long as stem of first. Spermathecae two, almost equal, pyriform.

Male.-

Length about 2 mm. TR about 1.2 in fore leg, 0.6 in middle leg and 0.8 in hind leg. Palps short, slender, third segment only slightly swollen, with rather shallow sensorium containing sessile sensilla. Antennae with basal flagellar segments 3-6 wider than long and segments 7-10 longer than wide; distal four segments elongate with segment 11 longest; AR about 1.1. Hypopygium with sternite 9 slightly more than half as long as wide, tergite 9 about half as long as wide; parameres with basimeres about 1½ times as long as wide and telomeres shorter than basimeres, curved; aedeagus V-shaped, bearing outward-turning hooklets at tip; claspettes an arch, narrowly separated at base, with broad arms and union moderately thick, the latter less heavily sclerotized.

The above diagnosis is preliminary and will be revised when other species are added to the subgenus .

Forcipomyia (Schizoforcipomyia) lerouxi CHAN NEW SPECIES

Larva.-

Length of full-grown fourth instar 2.94 mm. Color in life yellow brown with intestinal contents brown.

Head brown to dark brown; eyes small, disappearing; p, q and t hairs simple, long; p hair with secondary short seta on tubercle; s seta absent; antennae with filament long, tapering, intermediate between those of Forcipomyia s. str. and Proforcipomyia (Fig. 18B). HR 1.60; OH/v 0.98; AR 3.89; qt/tu/uq 1.59: 1: 1.68; tt/ant 0.52; qq/eyes 0.35; qq/pp 0.50.

Prothoracic a and b setae with filament and tubercle in proportion of 3.86: 1 and 20 : 1 respectively; prothoracic pseudopod with distal half bifid, and length, width and depth in proportion of 2.24: 1.71: 1 and bearing on apex of each branch five black hooks (Fig. 18C).

Abdominal chaetotaxy as illustrated (Fig. 18A),that of abdominal segments 1-7 similar. Anal pseudopod (Fig. 18D) divided into two lobes, each lobe bearing eight hooks; anal blood gills four, outer pair unequally bilobed.

Cuticular armature confined to dorsum and dorsal half of pleura, consisting of small, short setae; ventral integument smooth.

Pupa (Female).-

Length 2.38 mm. Color as in larva but dark just prior to emergence of adult.

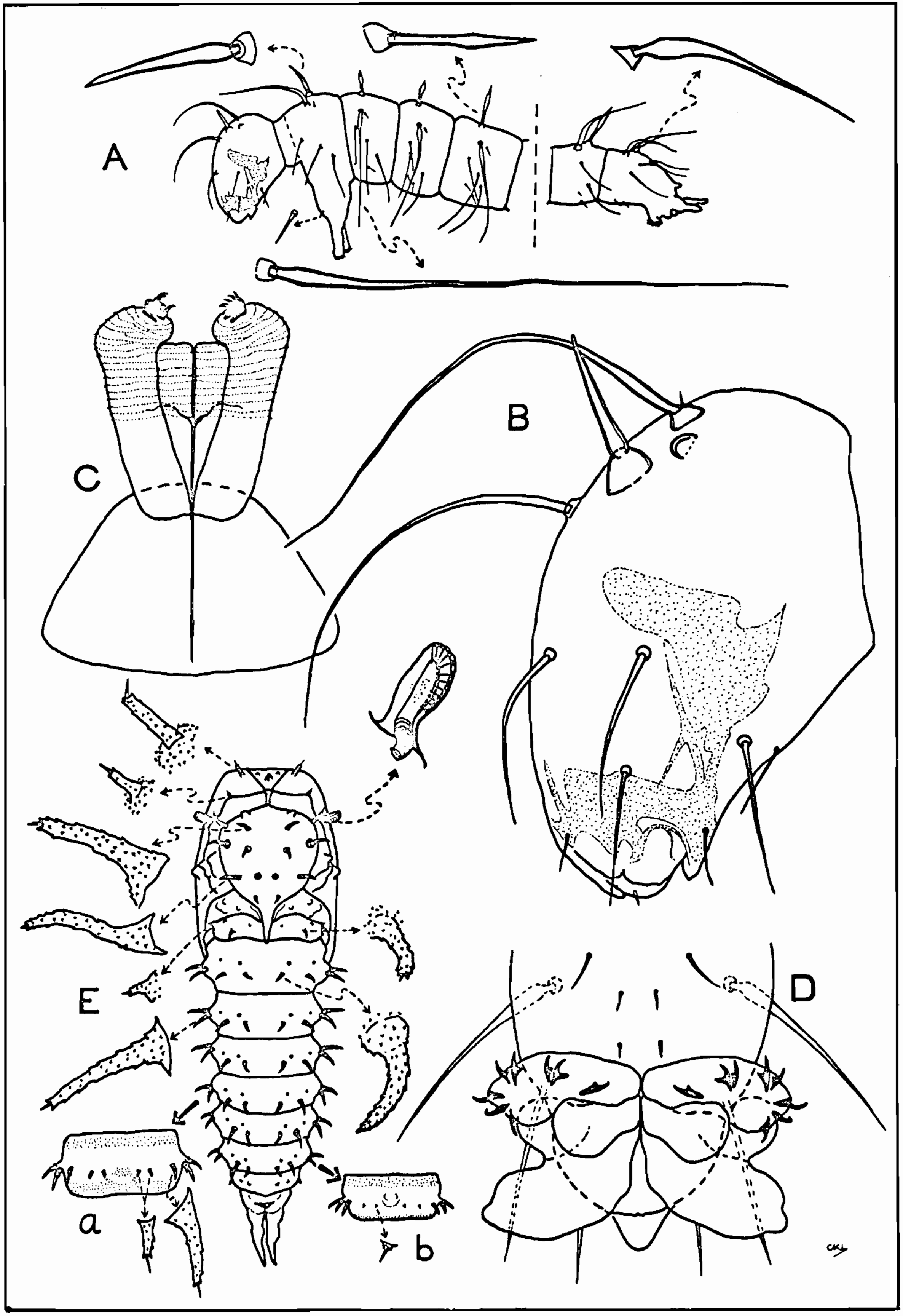
Median head sclerite with three tubercles, median elongate, lateral rudimentary; lateral sclerites each with an elongate tubercle bearing a short seta at apex. Cephalothorax 1.71 times as long as its greatest width. Head length to thorax length 0.17: 1 in dorsal aspect and 0.41: 1 in ventral aspect.

Thorax bearing seven pairs elongate and two pairs rudimentary tubercles on dorsum (Fig. 18E) arranged in six transverse rows; elongate tubercles in first, third and fifth row each bearing a short seta.

Fig. 18. Forcipomyia (Schizoforcipomyia) lerouxi n. sp.

A-D, Fourth-instar larva:
  A, Larva, lateral view
  B, Head
  C, Prothoracic pseudopod
  D, Anal pseudopod
  E, Pupa: dorsal view
    a, Fifth abdominal segment, ventral view
    b, Seventh abdominal segment, ventral view

Fig. 18



Prothoracic horn (Fig. 18E) club-shaped, short, with row of about 11 spiracular papillae curving around posterior edge; horn length to width 2.15: 1: ratio of tracheal length to horn length 0.79.

Abdominal segments 2-7 each with four pairs of tubercles on dorsum, arranged in two rows of two pairs per row, anterior row rudimentary and posterior row elongate, inner pair of which are non-setate and outer pair with short setae; segment 8 with two pairs rudimentary tubercles on dorsum; segment 1 with four pairs tubercles, two pairs rudimentary; segments 2 and 8 each with two pairs lateral tubercles and segments 3-7 each with three pairs; segments 3-8 each with two pairs of ventral tubercles.

Adult Female.-

Length 1.53 mm. Wing (Fig. 19C) 0.83 x 0.35 mm.

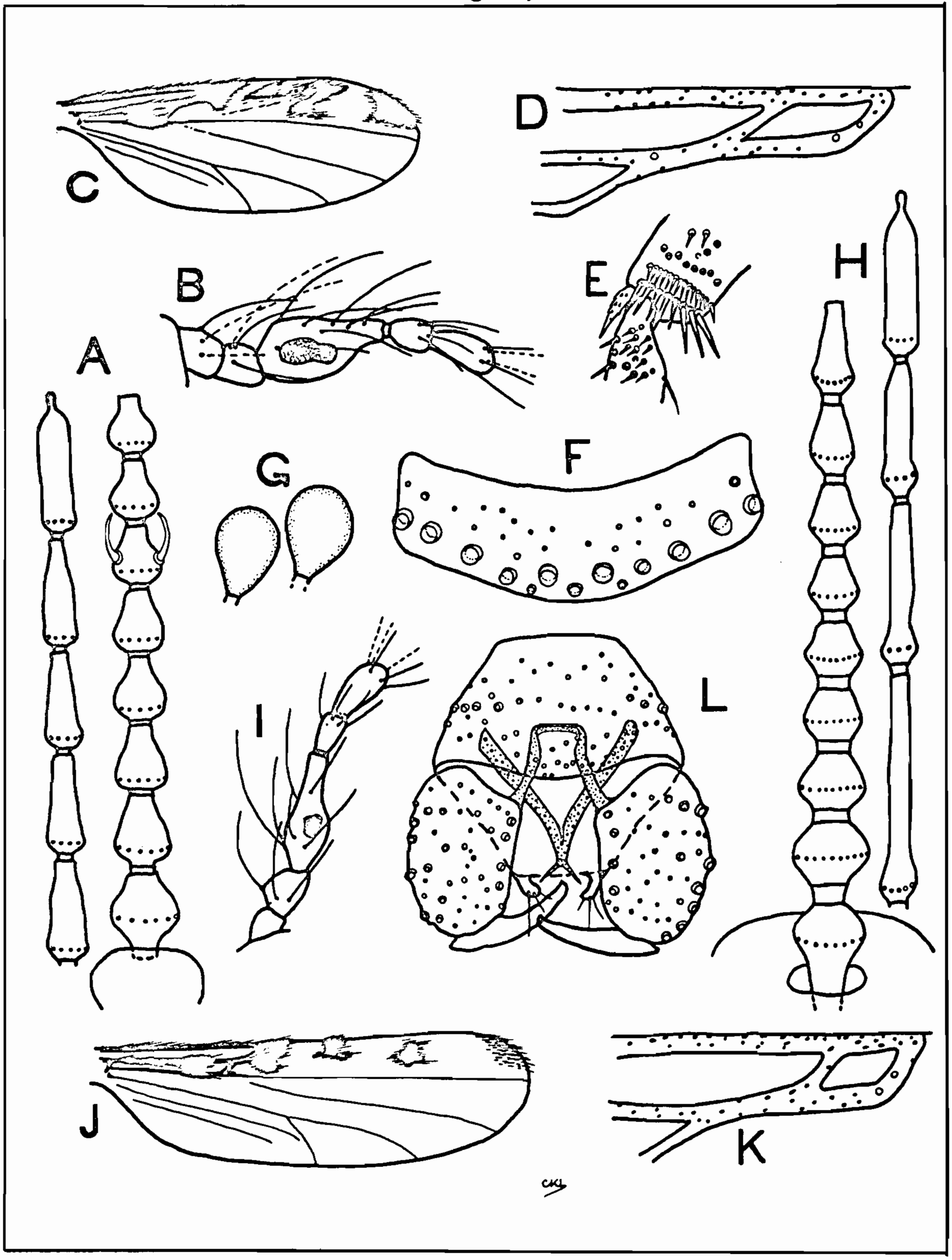
Head with antennae and mouthparts brown, eyes black, practically contiguous dorsally. Maxillary palp (Fig. 19B) large, base of last segment at tip of proboscis; segment 3 very stout at basal three-quarters and narrow at apical quarter, bearing large, very deep sensory pit; PR 2.09. Antenna (Fig. 19A) uniformly brown, with segments 2-9 pyriform and segments 10-14 elongate; AR 1.00. Hairs on vertex long and bent forward.

Thorax brown with scutellum bearing 11 strong bristles (Fig. 19F). Legs brown, with fore tibiae bearing a row, and mid and hind tibiae bearing two rows, of long setae; basal two-thirds of femur, two- and four-fifths of tibia and basal ends of tarsal segments pale yellow; TR 1.46 in fore leg, 0.80 in middle leg and 0.96 in hind leg; apical tibial comb with nine bristles.

Fig. 19. <u>Forcipomyia</u> (<u>Schizoforcipomyia</u>) <u>lerouxi</u> n. sp.

- A-G, Adult female:
  - A, Antenna
  - B, Maxillary palp
  - C, Wing
  - D, Anterior wing venation
  - E, Hind tibial comb
  - F, Scutellum
  - G, Spermathecae
- H-L, Adult male:
  - H, Antenna
  - I, Maxillary palp
  - J, Wing
  - K, Anterior wing venation
  - L, Genitalia

Fig. 19



Wings brown, densely clothed with hair-like and scale-like trichiae, and bearing five dark spots as illustrated (Fig. 19C); CR 0.64. Venation: vLR 1.19: 1: 1.76; rs/r_1 1.69; first radial cell obliterated, second radial cell moderately wide, 1.43 times as long as first; m_{3+4} less than twice length of cu_1 (1.87: 1); fmcu ending under about middle of second radial cell (Fig. 19C). Halteres light brown.

Abdomen brown; spermathecae (Fig. 19G) two, almost equal, pyriform, measuring 55.20 x 37.95 μ and 51.75 x 34.50 μ.

Adult Male.-

Length 1.95 mm. Wings 1.05 x 0.32 mm. Color brown to yellow-brown.

Head brown, with eyes and antennal scapes dark; antennal segments lighter brown, antennal plume dark brown, reaching to end of segment 13; AR 1.06; proboscis light brown; maxillary palps short, slender, third segment longest, slightly swollen at basal half and containing rather shallow, small sensorium with sessile sensilla; PR 3.07.

Thorax dark brown, with scutellum bearing 11 strong bristles as in female. Legs brown, with fore tibiae bearing a row of long setae, mid and hind tibiae bearing two rows of very long setae; all tibiae with basal third and tip pale yellow, second and third tarsal segments of hind leg pale yellow at basal end; TR 1.24 in fore leg, 0.61 in middle leg and 0.75 in hind leg; apical tibial comb with eight bristles (including spur).

Wings brown, clothed with numerous scales and bearing four dark spots on anterior border (Fig. 19J); CR 0.43. Venation vLR 1.14: 1: 1.66; rs/r_1 1.67; first radial cell obliterated, second radial cell somewhat narrow, slightly longer than first (1.20: 1) (Fig. 19K); fmcu under slightly beyond tip of costa; m_{3+4} about $2\frac{1}{2}$ times length of cu_1 (2.63: 1).

Abdomen light brown with genitalia darker brown and bearing long setae on basimeres. Genitalia (Fig. 19L): sternite 9 more than half as long as wide (0.57: 1); tergite 9 about half as long as wide (0.48: 1). Parameres with basimeres large, broad, about $1\frac{1}{2}$ times as long as wide (1.68: 1), and telomeres boat-shaped, relatively slender, shorter than basimeres (0.73: 1) and 4.5 times as long as wide. Aedeagus a V, with distal tip bearing small outward-turning processes (Fig. 19L). Claspettes arch-like, narrowly separated at base, basal arms and basal union moderately thick, the latter less heavily sclerotized; b/c/b in proportion of 1.30: 1: 1.30.

<u>Holotype (fourth instar larva)</u>: Collected between bark and wood of decaying stem of Angsana (<u>Pterocarpus indicus</u> Willd.) tree, at Wallace Way, Singapore. Deposited in Lyman Entomological Museum, Macdonald College, Quebec, Canada.

<u>Paratypes</u>.- Collected from same habitat and locality as holotype; 2 pupae, 1 male and 1 female, deposited in Lyman Entomological Museum.

This species is close to <u>Forcipomyia</u> (<u>Metaforcipomyia</u>) <u>fuscimaculata</u> Hardy (1960) and <u>F</u>. (<u>F</u>.) <u>penniornata</u> Tokunaga and Murachi (1959) in structure of the male genitalia, especially in the V -shaped aedeagus of the former and T-shaped aedeagus of the latter, both with outward-turning hooks or carinae at the tip, but differs from both in lacking claspette processes.

Hardy's (1960) diagnosis of <u>Forcipomyia</u> <u>fuscimaculata</u> as a species of <u>Metaforcipomyia</u> is certainly a misidentification, since the claspette processes do not unite in mid-line and the aedeagus is not broadly bilobed and serrate at the distal tip.

Other Species.-

From the structure of the aedeagus the following species may be recognized as belonging to this subgenus:

Forcipomyia (Forcipomyia) penniornata Tokunaga and Murachi (1959);
Insects of Micronesia 12(3): 163

Forcipomyia (subgenus B) fuscimanus Kieffer (1921);
Philippine Jour. Sci. 18: 557
Tokunaga and Murachi (1959),
Insects of Micronesia 12(3): 216

Forcipomyia (Metaforcipomyia) fuscimaculata Hardy (1960);
Univ. Hawaii Press 10: 170

5. SUBGENUS WARMKEA SAUNDERS (1956)

Subgenus type bicolor Saunders (1956)

Diagnosis.-

The following diagnosis is taken from Saunders' (1956) "Revision of the genus Forcipomyia":

"Larva.-

Colorless with light or dark head, prognathous; antennae as in subgenus Forcipomyia. Chaetae of body considerably reduced in number and size, some bifid or multiple; a hairs minute, spear-shaped. Prothoracic pseudopod abruptly conical, transversely ridged and finely setulose, bearing at tip three pairs long, curved, hyaline hooklets, three pairs short, black hooklets, and one pair short sinuous processes in middle. Posterior pseudopod a transverse ridge bearing large, dark hooks arranged in the usual anterior row of five pairs and posterior row of four pairs, but crowded together on either side of median line. Cauda short, bluntly conical or more tapering, finely setulose. Anal blood gills two, double. No cuticular armature.

Pupa.-

With various knobby and spiny processes on thorax and abdomen. Prothoracic horns broad at base, projecting to angular knob on posterior surface; neck narrow, head rounded, bearing numerous spiracular papillae in row over top. Genital processes of male dorsal. Larval exuviae not retained.

Adults.-

TR 1.25-1.75. Lightly-built flies with pale coloration, more slender and less bristly than most *Forcipomyia* adults. Antennal segments, particularly of female, more elongate than in any other subgenus, with fine curved hyaline sensory hairs on segments 3-10; marked increase in length of segments at 11. Palpal segments 4 and 5 partially or completely fused; sensorium on segment 3 a group of capitate sensilla without enclosing chitinous ring or cylinder. Wings thinly clothed with macrotrichiae, unmarked; costa reaching two-thirds the length of the wing, second radial cell closed or almost closed, narrow, double the usual length in subgenus *Forcipomyia*. Legs slender, moderately bristly, devoid of lanceolate hairs; claws of female broad at middle; empodium well developed in both sexes. Spermatheca one. Male genitalia with same general plan as in subgenus *Forcipomyia*; parameres (*claspettes*) slender, with hooked tips extending beyond aedeagus; dististyles (*telomeres*) slender, strongly bowed with swollen base in two species, but straight and stout in other two, *and stout at base and narrow and curved at tip in a third*."

Species described in all stages.-

aeria Saunders (1956); Can.J.Zool. *34*: 677

bicolor Saunders (1956); Can. J. Zool. *34*: 675

malayae Saunders (1956); Can. J. Zool. 34: 678

spinosa Saunders (1956); Can. J. Zool. 34: 676

tuberculata Saunders (1956); Can. J. Zool. 34: 677

Other species.-

One species from Malaya (unnamed) (Saunders,1956); Can. J. Zool. 34: 671

One species from Florida and Puerto Rico (unnamed) (Saunders 1956); Can. J. Zool. 34: 671

F. GENUS LASIOHELEA KIEFFER (1921)

1. DIAGNOSIS

Larva.-

Small to moderately large, typically orange. Head small, hypognathous, vertex without p hairs, replaced by variable number of paired tubercles; antennae normal in position, small or reduced to basal ring or higher tubercle filled by chitinous disk flanked by reduced flagellum; eyes rather large, typically with ocular seta. Body segments bearing typically minute or "torch-like" chaetae. Prothoracic pseudopod an undivided cushion or divided in one rare case, bearing variable number of hooklets. Anal pseudopod a transverse ridge bearing one or two rows of hooklets. Cauda absent. Typical habitat algae and moss on decaying wood.

Pupa.- Head with median sclerite bearing three tubercles. Thorax and abdomen with variable number of small tubercles, usually very many. Prothoracic horn small, narrow basally, broader apically and bearing spiracular papillae of variable number and shape. Male sexual processes ventral. Larval exuviae retained or not retained.

Adult Female.- Small to rather large. Basal flagellar segments of antenna discoidal, subspherical or short-oval, without neck parts; distal five segments distinctly elongate or distal four moderately elongate or distal five segments gradually elongate, without abrupt change between segments 9 and 10. Maxillary palp distinctly five-segmented, with segment 3 bearing sensorium or scattered sensilla. Wings unadorned, with rather dense macrotrichia, bare areas adjoining veins usually distinct; costa ending about middle or distinctly beyond middle of wing; first radial cell closed, second radial cell narrowly open or practically closed, short or elongate. Empodium and claws normal. TR of hind leg usually larger than 2.0 and less than 3.0.

Adult Male.-

Basal flagellar segments of antenna usually flask-shaped, distal four segments usually distinctly elongate. Genitalia with aedeagus complicated, with tendency towards bipartitism; claspettes variable, slender, arch-like with basal union without processes or basal arm with slender or triangular processes, or with club-shaped processes; ninth sternite with or without membranous window.

2. KEYS TO LASIOHELEA SUBGENERA

LARVA

1. Antenna reduced to basal ring or higher socle bearing minute flagellum.............................Thyridomyia

Antenna normal or well-developed............................. 2

2(1). Antenna prominent with large socle placed high on front..................................... Synthyridomyia

Antenna normal in position, socle not large...................... 3

3(2). Body with a and b setae torch-like...................Lasiohelea

Body with a and b setae not torch-like......................... 4

4(3). Anal pseudopod with single row of six strong black hooklets....................................*Dacnoforcipomyia*

Anal pseudopod with a large number of hooklets......New subgenus (Lane's *Lasiohelea stylifer* Lutz)

PUPA

1. Larval exuviae not retained.. 2

Larval exuviae retained.. 3

2(1). Prothoracic horn with an ellipse of spiracular papillae whose roots meet centrally in a deep fissure...*Synthyridomyia*

Prothoracic horn with multiple spiracular papillae in row across end...*Thyridomyia*

3(1). Body with dorsal tubercles and bearing short, stellate-tipped setae...............................*Dacnoforcipomyia*

Body with dorsal tubercles small or elongate and bearing simple short setae.........................New subgenus (Lane's *Lasiohelea stylifer* Lutz)

ADULT FEMALE

1. Antennal segments gradually elongating, without abrupt change between segments 9 and 10................*Synthyridomyia*

Antennal segments with abrupt change in length between segments 9 and 10 or with moderate elongation of segment 10 or 11.................................. 2

2(1). Wing costa reaching beyond middle of wing but second radial cell open and short........................*Thyridomyia*

Wing costa reaching distinctly beyond middle of wing, second radial cell usually practically closed and elongated................................*Dacnoforcipomyia*
Lasiohelea
New subgenus
(Lane's *Lasiohelea stylifer* Lutz)

ADULT MALE

1. Ninth sternite with membranous window...................*Thyridomyia*

Ninth sternite without membranous window......................... 2

2(1). Claspettes without basal union, processes club-shaped or hook-shaped............................<u>Synthyridomyia</u>

Claspettes with basal union, processes absent...................... 3

3(2). Claspettes arch-like, slender, with delicate anterior membranous flange, and short anterior projections at corners of basal union........<u>Dacnoforcipomyia</u>

Claspettes arch-like, slender, without anterior membranous flange, nor projections at corners of basal union...............................<u>Lasiohelea</u>
New subgenus
(Lane's <u>Lasiohelea stylifer</u>
Lutz)

3. SUBGENUS <u>SYNTHYRIDOMYIA</u> SAUNDERS (1956)

Subgenus type <u>acidicola</u> Tokunaga (1937)

Diagnosis

The following diagnosis of the immature stages is taken from Saunders' (1956) paper on the revision of the genus <u>Forcipomyia</u>.

"<u>Larva</u>.-

Colorless or strong orange in the two species known. Head hypognathous, dark; antennae prominent with large basal tubercles placed high on frons; eyes large, with slender ocellar hair; vertex with paired blunt tubercles; frons wrinkled; no distinctive <u>p</u> or <u>q</u> hairs. Body segments with small dorsal and dorsolateral rounded tubercles bearing minute multiple chaetae; no <u>a</u> hairs or long setae. Prothoracic pseudopod large, undivided, bearing distally many slender and stouter hooklets disposed in several rows. Posterior pseudopod a transverse ridge bearing two rows of black hooklets. Cauda absent.

<u>Pupa</u>.-

Small tubercles on head, thorax and abdomen, no long setae. Prothoracic horns slender, slightly enlarged distally to accommodate an ellipse of spiracular papillae whose roots meet centrally in a deep fissure. Male genital processes ventral. Exuviae not retained."

Adult Female.-

Small flies, not exceeding 1.5 mm. in length. Antennae with basal segments subspherical, elongating gradually, without abrupt change between segments 10 and 11; distal five segments may be provided with reticular relief on surface as in Dasyhelea species. Palpal segments distinctly five-segmented, segment 3 with deep sensorium or with surface group of capitate sensillae. Wings moderately clothed with macrotrichia, with very slender non-striped scales or without scales; costa ending at about middle of wing; first radial cell absent or very narrow, second radial cell open; bare areas along veins almost absent. Legs with empodia long and slender; TR greater than 2.0, less than 3.0. Single spermatheca.

Adult Male.-

Genitalia with claspettes club-shaped or strongly hook-shaped; ninth sternite emarginate or with a semicircular caudal incision; aedeagus subdivided into paired lateral sclerites as in subgenus Lasiohelea or undivided, square and broad.

Species described in all stages.-

Only one species has been described in all stages -- acidicola whose early stages were taken on the shores of a highly acidic (pH 1.4) volcanic lake in Honshu, Japan.

Other species.-

Species identified by the male genitalia include:

Ceratopogon murinus Winnertz (1852); Saunders (1925),
Parasitology 17: 274

Forcipomyia corsoni Macfie (1926); Bull. Entomol. Res. 16: 355

Forcipomyia knockensis Goetghebuer (1938); Bull. Ann. Soc. Entomol. Belge 78: 375

Forcipomyia tenuiforceps Macfie (1939); Rev. Entomol. Rio de Janiero 10: 167

Forcipomyia longitarsus Tokunaga (1940); Tenthredo 3: 92

Lasiohelea kii Tokunaga (1940); Tenthredo, 3: 107

Forcipomyia moascari Macfie (1943); Proc. Roy. Entomol. Soc. London, 42: 147

Thyridomyia colemani Wirth (1952); Univ. Calif. Publ.Entomol. 9: 146

Thyridomyia sanctaeclarae Wirth (1952); Rev. Chilena Entomol. 2: 90

Synthyridomyia unituberculata Tokunaga (1959); Insects of Micronesia 12(3): 90

4. SUBGENUS THYRIDOMYIA SAUNDERS (1925)

Subgenus type palustris Saunders (1925)

a. DIAGNOSIS

Larva.-

Head hypognathous; eyes rather large with or without ocular seta; antennae reduced to basal ring or socle bearing minute flagellum. Prothoracic pseudopod undivided, usually with three hyaline apical hooklets and variable number of other smaller hooklets; or divided with few hooklets on each ramus; body segments with many low tubercles. Cauda absent.

Pupa.-

Head, thorax and abdomen with many small low tubercles. Prothoracic horn short, usually broad distally and bearing few spiracular papillae in row across end. Male sexual processes ventral.

Adult Female.-

Basal antennal segments subspherical, slightly transverse; moderate elongation of segments usually at 11, rarely at 10. Maxillary palp distinctly five-segmented, segment 3 with sensorium or scattered sensillae. Wings unadorned, with rather dense macrotrichia; costa reaching beyond middle of wing, first radial cell closed, second open, usually short, rarely elongate. Empodia and claws normal. One spermatheca.

Adult Male.-

Basal flagellar segments usually flask-shaped, distal four segments elongate. Maxillary palp slender, distinctly five-segmented, segment 3 as in female. Wings, empodia and claws as in female. Genitalia with elongated ninth segments bearing membranous window of variable shape, usually like Moorish arch; claspettes without basal union, with triangular or slender processes, the latter united or separate; aedeagus complicated, tending towards bipartite condition, usually with two slender median sclerites.

b. Description of New Species

Lasiohelea (Thyridomyia) vertexcava CHAN NEW SPECIES

Larva.-

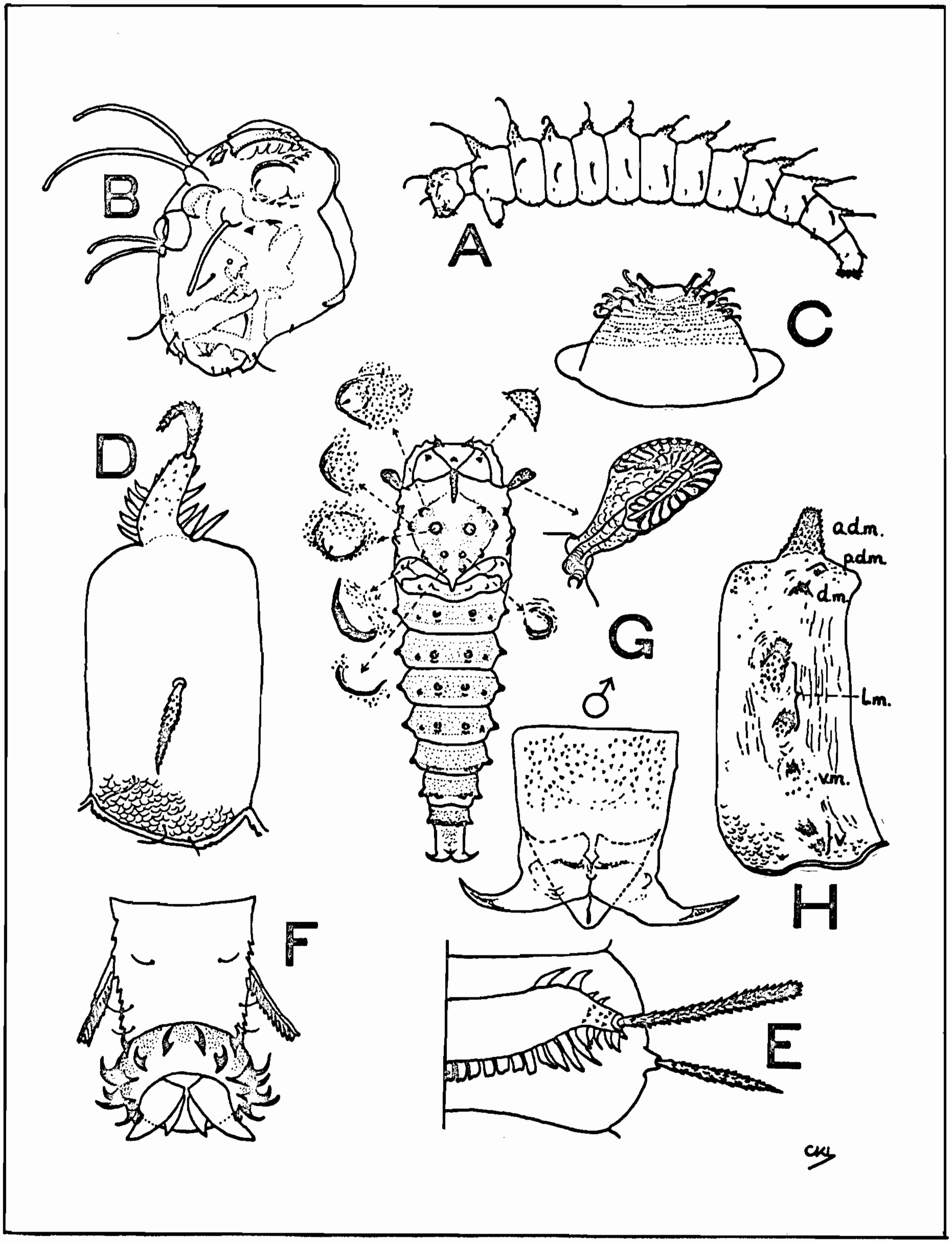
Length of fourth instar larva (Fig. 20A) 1.59 mm. Color orange pink except head which is dark brown to black.

Head (Fig. 20B) small, with three pairs of low prominences on vertex, one small and one large admedian pair and one large pair lateral to the large admedian pair, the two large pairs bordered by flap-like projections. On each side of the head and postero-ventral to the s

Fig. 20. <u>Lasiohelea</u> (<u>Thyridomyia</u>) <u>vertexcava</u> n. sp.

- A-F, Fourth-instar larva:
  - A, Larva, lateral view
  - B, Head
  - C, Prothoracic pseudopod
  - D, First abdominal segment, lateral view
  - E, First abdominal segment, dorsal view
  - F, Anal pseudopod
- G-H, Pupa:
  - G, Dorsal view
  - H, Sixth abdominal segment, lateral view

Fig. 20



hairs are two pairs of small protuberances. Eyes prominent with hyaloid dome and basal pigmented portion; antennae typically thyridomyian, without flagella and close to the eyes as in Forcipomyia aspinosa Saunders; setae as in diagnosis (Fig. 20B). HR 1.44; qt/ts/sq in proportion of 1.56: 1.50: 1; tt/ant 0.49; qq/eyes 0.48; qq/ss 0.39.

On dorsum of each body segment except last, the a hairs are situated on long, tapering tubercles (Figs. 20A, 20D, 20E) as in Forcipomyia palustris Saunders, the hairs connected across dorsum by strong sclerotized bands flanked posteriorly by spines the central ones of which are shorter and chisel-shaped (Fig. 20E). Thoracic a hairs each bears a small seta at base on ventral side (Fig. 20A). b hairs placed laterally, situated on conical bases and covered with spinules as in a hairs, except that apices are pointed (Fig. 20D, 20E).

First abdominal setae a and b with filament and tubercle in proportion of 1.90 and 8.00 respectively. Prothoracic pseudopod (Fig. 20C) with length, width and depth in proportion of 1.33: 1.73: 1 and bearing about 24 slender hooks in three rows. All body segments except last bear h, i and g setae (Figs. 20A, 20D, 20E). Cuticular armature scale-like (Fig. 20D). Posterior pseudopod with nine pairs dark, curved, hooks arranged in two rows and two pairs of unequal anal papillae. Cauda absent.

Pupa.-

(all measurements are for the female).

Length 1.40 mm. Color orange, orange-pink in thorax but dark just prior to emergence of adult.

Median head sclerite (Fig. 20G) with three well-developed tubercles.

anterior pair setulose; lateral sclerites each with single setulose seta; ventro-median tubercles minute, ventro-lateral tubercles absent. Cephalothorax 1.42 times longer than its greatest width. Length of head to thorax in proportion of 0.48: 1 in ventral aspect and 0.23: 1 in dorsal aspect. Ratio of cephalothorax to abdomen 0.60.

Thorax (Fig. 20G) bearing an anterior median ridge and seven pairs of tubercles, two anterior pairs of which are setulose. Prothoracic respiratory horn funnel-shaped with broad apex and narrow base, and bearing about thirty-nine spiracular papillae in double palisade; its length about twice greatest width; horn tracheal length to horn length 0.72: 1 and tracheal length to width in proportion of 10.29: 1.

Abdominal segment 1 with two pairs of rudimentary tubercles, segments 2-8 with three pairs of tubercles on dorsum (Fig. 20G) which are the anterior dorso-median (a.d.m.), posterior dorso-median (p.d.m.) and dorso-marginal (d.m.) tubercles (Fig. 20H); segments 2-4 each with three pairs, and segments 5-8 each with two pairs, of lateral marginal tubercles (l m., Fig. 20H); segments 3-7 each with one pair ventro-marginal tubercles (v.m., Fig. 20H). Terminal processes directed outwards, sharply pointed in both sexes. Male sexual processes ventral, short and united terminally (Fig. 20G).

Adult female.-

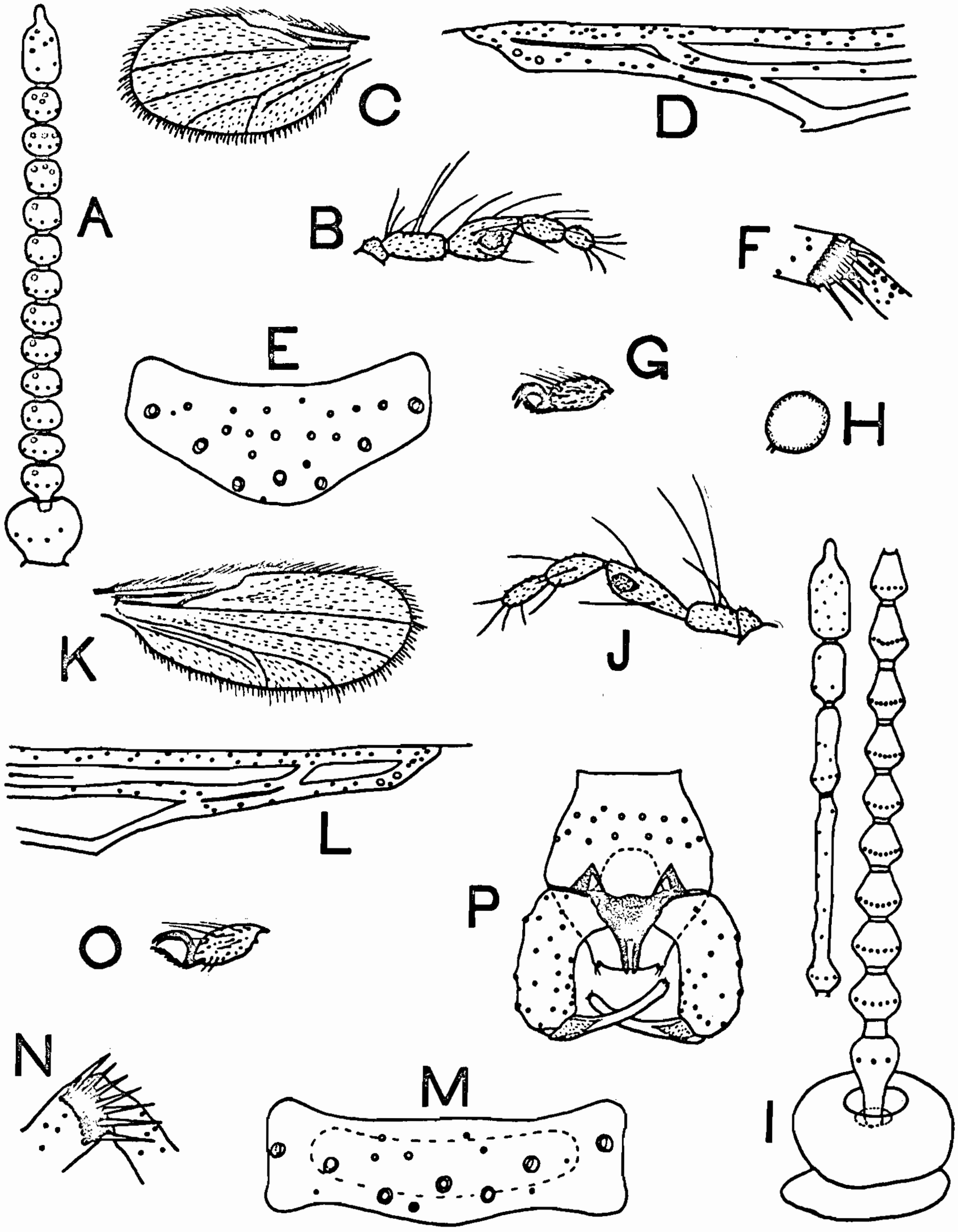
Length 0.90 mm. Wing (Fig. 21C) 0.53 x 0.29 mm.

Head with antennae and mouthparts brown; eyes and pedicels dark brown. Antennal segments (Fig. 21A) subglobular with only last segment distinctly longer than the rest; flagellar segments from base to tip in proportion of 6.5: 5: 5: 5:5: 5: 4.5: 4.5: 5: 5: 5: 5.5: 12; AR 0.78. Maxillary palp (Fig. 21B) with segments in proportion of 4:

Fig. 21. Lasiohelea (Thyridomyia) vertexcava n. sp.

- A-H, Adult female:
  - A, Antenna
  - B, Maxillary palp
  - C, Wing
  - D, Anterior wing venation
  - E, Scutellum
  - F, Hind tibial comb
  - G, Last segment of hind leg
  - H, Spermatheca
- I-P, Adult male:
  - I, Antenna
  - J, Maxillary palp
  - K, Wing
  - L, Anterior wing venation
  - M, Scutellum
  - N, Hind tibial comb
  - O, Last segment of hind leg
  - P, Genitalia

Fig. 21



11: 13: 8: 5; PR 1.86; segment 3 bearing large, shallow sensory pit.

Thorax brown, scutellum (Fig. 21E) with seven strong bristles. Legs pale brown, with TR 2.90 in fore leg, 2.50 in middle leg and 3.18 in hind leg; claws and empodia (Fig. 21G) normal; hind tibia with six tibial spines.

Wings brown; CR 0.53. Venation: vLR 1.22: 1: 2.59; rs/r_1 2.25; first radial cell short, obliterated, second radial cell very narrow, twice length of first (2.00: 1); fmcu under about $\frac{2}{3}$ of second radial cell; m_{3+4} about twice length of cu_1 (2.07: 1). Halteres brown.

Abdomen brown. Spermathecae (Fig. 21H) single, oval, measuring 34.50 μ by 31.05 μ.

Adult Male.-

Length 1.07 mm. Wing (Fig. 21K) 0.66 x 0.26 mm. Color as in female.

Antennal flagellar segments (Fig. 21I) from base to tip in proportion of 15.5: 8: 8: 8: 7.5: 7: 7.5: 7.8: 8: 32: 15: 9.5: 15.5; AR o.84. Maxillary palp (Fig. 21J) with segments in proportion of 4: 8: 15: 8: 6; segment 3 with small, deep pit just beyond middle; PR 3.13.

Thorax brown, with scutellum (Fig. 21M) bearing 6-7 large bristles. Legs pale brown, with TR 2.97 in fore leg, 2.26 in middle and 2.76 in hind leg; claws long, slender, empodia fine (Fig. 21 O), hind tibia with 6-7 tibial spines (Fig. 21N).

Wings brown, CR 0.45. Venation: vLR 1.22: 1: 2.35; rs/r_1 1.88; first radial cell short, obliterated (Fig. 21L), second radial cell moderately wide; RR 0.97; fmcu under about tip of costa; m_{3+4}/cu_1 2.50.

Genitalia (Fig. 21P); sternite 9 about $\frac{3}{4}$ as long as wide (0.77: 1), tergite 9 about half as long as wide (0.53: 1). Parameres with basimeres curved at basal third and less than $2\frac{1}{2}$ times as long as wide (2.30: 1), and with telomeres slender, curved at middle and with tip rounded, more than 5 times as long as greatest width (5.19: 1); telomeres slightly shorter than basimere (0.90: 1). Aedeagus funnel-shaped, caudo-lateral shoulders composed of slender oblique sclerites. Claspettes a triangle, with broad bases and recurved slender sclerites (the equivalent of basal union in Forcipomyia (Forcipomyia) s. str. forms).

Holotype (fourth instar larva).- Collected on moss and liverworts on clay bank at Wallace Way, Singapore. Deposited in Lyman Entomological Museum, Macdonald College, Quebec, Canada.

Paratypes.- Collected in same habitat and locality as holotype; 2 larvae, 2 males and 2 females and 16 associated pupal exuviae deposited in Department of Zoology, University of Singapore.

In general appearance the larva of this species resembles that of Forcipomyia (Thyridomyia) palustris Saunders (1925), especially in the short, deep body segments and the long a and b setae on prominent elongated tubercles. It differs, however, in the shape and number of prominences on the head and in the somewhat shorter tubercles of the a and b setae. The pupa also resembles that of palustris in the large number of low dorsal tubercles on the thorax and abdomen, but differs in the shape, and number of spiracular papillae, of the prothoracic horn, and in the sharply pointed, outward-turning terminal processes. The male genitalia also resemble in general those of palustris but the basally curved basimeres immediately distinguish the two species apart.

Lasiohelea (Thyridomyia) rugosa CHAN NEW SPECIES

Egg.-

Elongate, ovoid, rounded anteriorly (micropylar end) and bluntly pointed posteriorly (Fig. 22A). Color black; exochorion smooth, without ornamentation. Measurements based on 10 eggs: 249.09 ± 8.42 µ long by 83.15 ± 5.26 µ wide.

Larva.-

Length of third instar 1.26 ± 0.04 mm. and 2.10 mm. in fourth instar. Color in life orange-red.

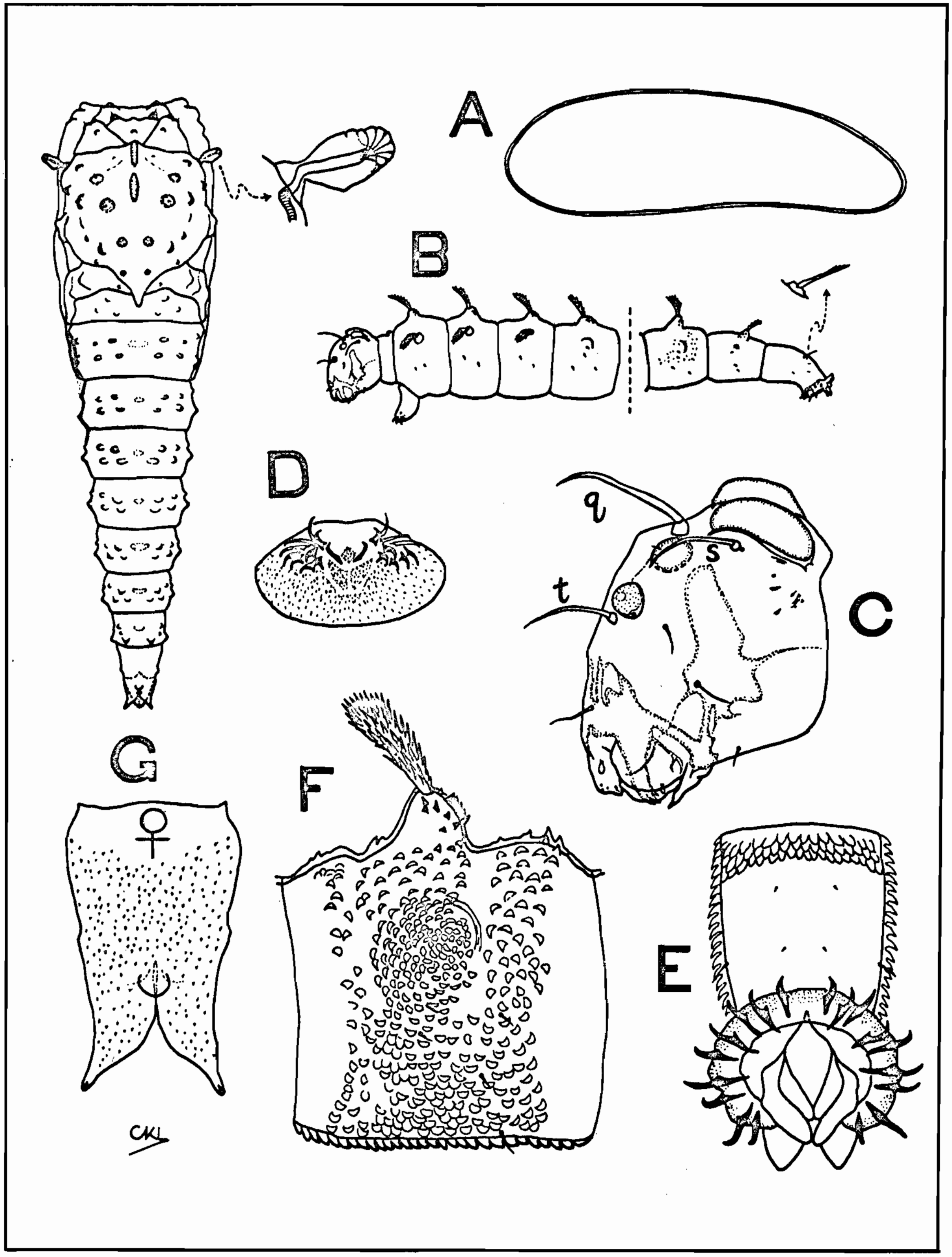
Head brown; chaetotaxy as in Thyridomyia palustris Saunders (1925), with two pairs of conspicuous prominences on vertex (Fig. 22C). Eyes large with ocular setae on inner margin; antennae typically thyridomyian, with very minute reduced flagella. HR 1.39 ± 0.04; qt: ts: sq in proportion of 1.96 ± 0.08: 2.36 ± 0.10: 1; tt/ant 0.45 ± 0.01; qq/eyes 0.53 ± 0.03; qq/ss 0.45 ± 0.02.

a setae on body segments short, stout and "torch-like" and borne on prominent tubercles (Figs. 22B, 22F); length of a filament to tubercle in proportion of 2.60 ± 0.28: 1. Seta b similar to a but found on thoracic segments only (Fig. 22B) and reduced to low prominences in other segments except last, where it is absent; b seta on prothorax with filament and tubercle in proportion of 2.76± 0.27: 1. Prothoracic pseudopod short, broad, undivided, furnished with four pairs of distal, slender, hyaline hooklets and six pairs short, stouter, black hooklets arranged in two rows, three to each row on each side (Fig. 22D); its length, breadth and depth in proportion of 1.33 ± 0.05: 1.46 ± 0.07: 1. Other smaller setae as illustrated (Figs. 22B, 22F).

Fig. 22. Lasiohelea (Thyridomyia) rugosa n. sp.

- A, Egg
- B-F, Fourth-instar larva:
  - B, Larva, lateral view
  - C, Head
  - D, Prothoracic pseudopod
  - E, Anal pseudopod
  - F, Third abdominal segment
- G, Pupa: dorsal view

Fig. 22



Pupa.-

Length 1.70 ± 0.12 mm. in female and 1.76 ± 0.10 mm. in male. Color as in larva but dark just prior to emergence of adult.

Median head sclerite with three low tubercles, anterior pair setulose; lateral sclerites each with single non-setulose, low tubercle. Cephalothorax 1.66 ± 0.22 times longer than its greatest breadth in female and 1.88 ± 0.03 times in male. Ratio of head length to thorax length 0.42 ± 0.02 (ventral aspect) and 0.25 ± 0.01 (dorsal aspect) in female and respectively 0.45 ± 0.02 and 0.30 ± 0.02 in male.

Thorax bearing eleven pairs of rudimentary tubercles and two median ridges (Fig. 22G), two anterior largest pairs setulose. Prothoracic horn (Fig. 22G) short, with narrow base and distinct posterior "heel" and bearing 5-8 spiracular papillae across rounded apex; 2-6 rudimentary papillae usually also present proximal to the normal distal ones; length of horn to greatest breadth 1.78 ± 0.15 in female and 1.82 ± 0.13 in male; tracheal length in horn to horn length 0.67 ± 0.01 in female and 0.64 ± 0.03 in male.

Abdominal segments with four pairs of low dorsal tubercles in segments 2-7 and three pairs in segments 1 and 8. Segments 2-8 with median elliptical cuticular marking. Cuticular armature with minute, fine setae (Fig. 22G). In female length, breadth and depth of third segment in proportion of 1: 1.92 ± 0.21: 1.89 ± 0.17 and that of last segment 1.26 ± 0.08: 1.00 ± 0.02: 1. In male, similar ratios for third segment 1: 1.90 ± 0.13: 1.87 ± 0.12 and for sexual processes 1.80 ± 0.15: 1.10 ± 0.08: 1 .

Adult Female.-

Length 1.23 ± 0.11 mm. Wings 0.70 ± 0.12 mm. by 0.34 ± 0.06 mm.

Head with antennae and mouthparts dark brown, eyes black. Maxillary palp slender with third segment bearing large, shallow sensory pit (Fig. 23B); PR 2.58 ± 0.29. Antenna uniformly brown, AR 1.10 ± 0.07 (Fig. 23A).

Thorax dark brown; scutellum with bristle arrangement as shown (Fig. 23L). Legs brown; fore TR 2.61 ± 0.08; mid TR 2.39 ± 0.08; hind TR 2.59 ± 0.15; claws and empodia normal (Fig. 23F); hind tibia with 7 or 8 tibial spines.

Wings (Fig. 23C) brown with veins dark brown; CR 0.52 ± 0.02. Venation: vLR 1.28 ± 0.07: 1: 2.50 ± 0.11; rs/r_1 1.94 ± 0.21: 1; first radial cell slit-like, obliterated, second radial cell somewhat narrow, slightly longer than first (1.34 ± 0.21: 1) (Fig. 23D); fmcu under about middle of second radial cell; m_{3+4} about twice length of cu_1 (1.91 ± 0.03: 1). Haltere with knobs white.

Abdomen brown; spermathecae (Fig. 23G) single, pyriform, measuring 49.85 ± 11.63 μ by 44.16 ± 11.56 μ and its duct 12.25 ± 0.48 μ.

Adult Male.-

Length 1.42 ± 0.10 mm. Wings 0.84 ± 0.14 mm. by 0.29 ± 0.04 mm.

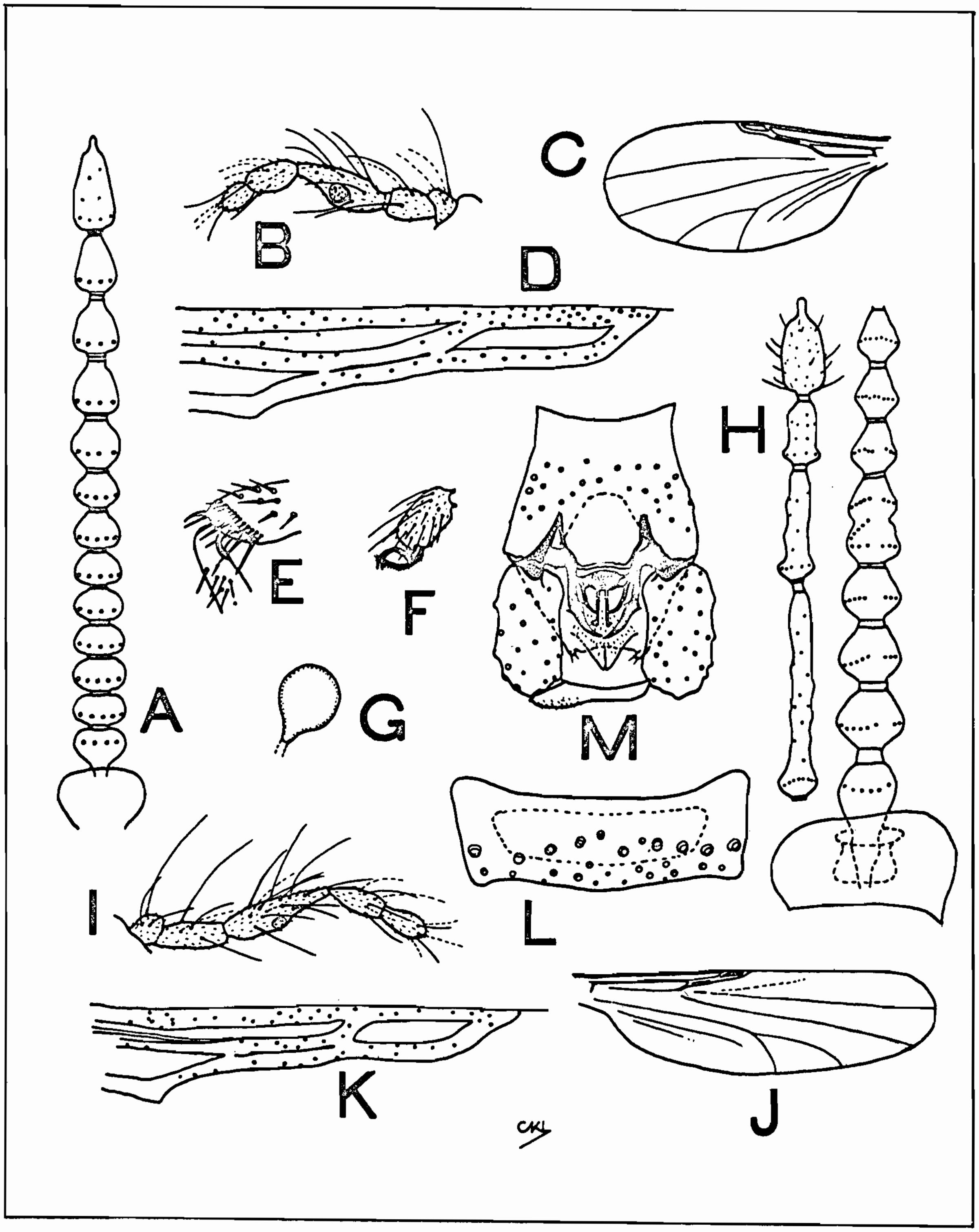
Head with antennae and mouthparts brown, eyes black. Maxillary palp (Fig. 23I) slender, with segment three bearing small, shallow sensory pit at middle; PR 3.67 ± 0.31. Antenna (Fig. 23H) brown, AR 0.96 ± 0.05.

Thorax dark brown; scutellum with bristle arrangement as shown (Fig. 23L). Legs brown; fore TR 2.82 ± 0.07; mid TR 2.32 ± 0.10;

Fig. 23. Lasiohelea (Thyridomyia) rugosa n. sp.

- A-G, Adult female:
  - A, Antenna
  - B, Maxillary palp
  - C, Wing
  - D, Anterior wing venation
  - E, Hind tibial comb
  - F, Last segment of hind leg
  - G, Spermatheca
- H-M, Adult male:
  - H, Antenna
  - I, Maxillary palp
  - J, Wing
  - K, Anterior wing venation
  - L, Scutellum
  - M, Genitalia

Fig. 23



hind TR 2.85 ± 0.16; claws and empodia normal; hind tibia with 6-8 tibial spines.

Wings (Fig. 23J) brown with veins dark brown; CR 0.47 ± 0.01. Venation: vLR 1.23 ± 0.01: 1: 2.21 ± 0.10; rs more than $1\frac{3}{4}$ times length of r_1 (1.86 ± 0.09: 1); first radial cell slit-like, obliterated; second radial cell only slightly narrow, shorter than first (0.89 ± 0.06) (Fig. 23K); fmcu under about tip of costa; m_{3+4} about $2\frac{1}{2}$ times length of cu_1 (2.28 ± 0.15: 1). Haltere with knob white.

Abdomen brown. Hypopygium (Fig. 23M) with sternite 9 slightly shorter than wide (0.84 ± 0.03: 1) and tergite 9 about half as long as wide (0.47 ± 0.03: 1). Basimere rather straight, slightly more than twice as long as wide (2.15 ± 0.08: 1); telomere about as long as basimere, curved and spoon-shaped at tip and somewhat constricted in middle, about six times as long as wide (6.04 ± 0.34: 1). Aedeagus close to Thyridomyia hamata Tokunaga and Thyridomyia aspinosa Saunders, V-shaped with lateral bars strongly curved anteriorly and not united at about middle; cross bar at anterior third broad, oval, with two median slender apically-hooked sclerites connected in the middle by slender curved structures running antero-laterally to middle of anterior lateral bars of aedeagus. Claspettes subtriangular,typically 'thyromydian', with broad base and narrow recurved processes; b/c/b 1.03 ± 0.09: 1: 1.03 ± 0.09.

Holotype (fourth instar larva).- Collected on rotting, moss-grown wood in Morgan Arboretum, Macdonald College, Quebec. Deposited in Lyman Entomological Museum, Macdonald College.

Paratypes.- Collected in same habitat and locality as holotype; 18 larvae (mainly third instars) 4 males, 2 females and 7 associated pupal exuviae in personal collections. Two larvae (third instars), 2 pupa exuviae (1 male, 1 female), 2 adult males and 2 adult females in L.G. Saunders' collection and several of all stages deposited in Lyman Entomological Museum.

The larva of rugosa in a very general way resembles that of Forcipomyia (Thyridomyia) aspinosa Saunders (1956) in the two pairs of elongate tubercles on the vertex of the head, the general arrangement of head chaetotaxy, and the "torch-like" a and b setae. It differs however in having simple q hairs (p hairs of Saunders, 1956) of the head, without feathered tip, in the arrangement of hooklets on the prothoracic pseudopod and in the more well-developed a and b "torch-like" setae. The pupa also resembles that of aspinosa in chaetotaxy of the abdomen, but differs in the shape and number of spiracular papillae of the prothoracic horn. The male genitalia too are close to those of aspinosa especially in the shape and structure of the aedeagus and 'triangular' claspettes, but differ in the stouter parameres. In these respects they also resemble the genitalia of Forcipomyia (Thyridomyia) hamata Tokunaga (1959) and Thyridomyia palustris Saunders (1925).

Rugosa is a very interesting species as it forms a definite link between Thyridomyia and Lasiohelea as will be evident from a discussion in a later section. From its larvae the writer originally identified rugosa as a Lasiohelea s. str. species from the orange-red color and hypersensitivity to molestation and, most of all, from the presence of "torch-like" a and b setae.

Lasiohelea (Thyridomyia) gossympina CHAN NEW SPECIES

Larva.-

It is regretted that larvae were not obtainable but from characters of the pupa and adults the larva can be expected to be typically thyridomyian but very spiny.

Pupa.-

Length 1.52 mm. in male and 1.55 mm. in female.

Median head sclerite (Fig. 24A) with three well-developed tubercles, anterior pair large, non-setate; lateral sclerites each with two tubercles, the posterior minute. Cephalothorax 1.86 times longer than its greatest width in male and 1.73 in female. Length of head to thorax in proportion of 0.50 in dorsal aspect and 0.24 in ventral aspect in male and respectively 0.44 and 0.18 in female. Ratio of cephalothorax to abdomen 0.69 in male and 0.60 in female.

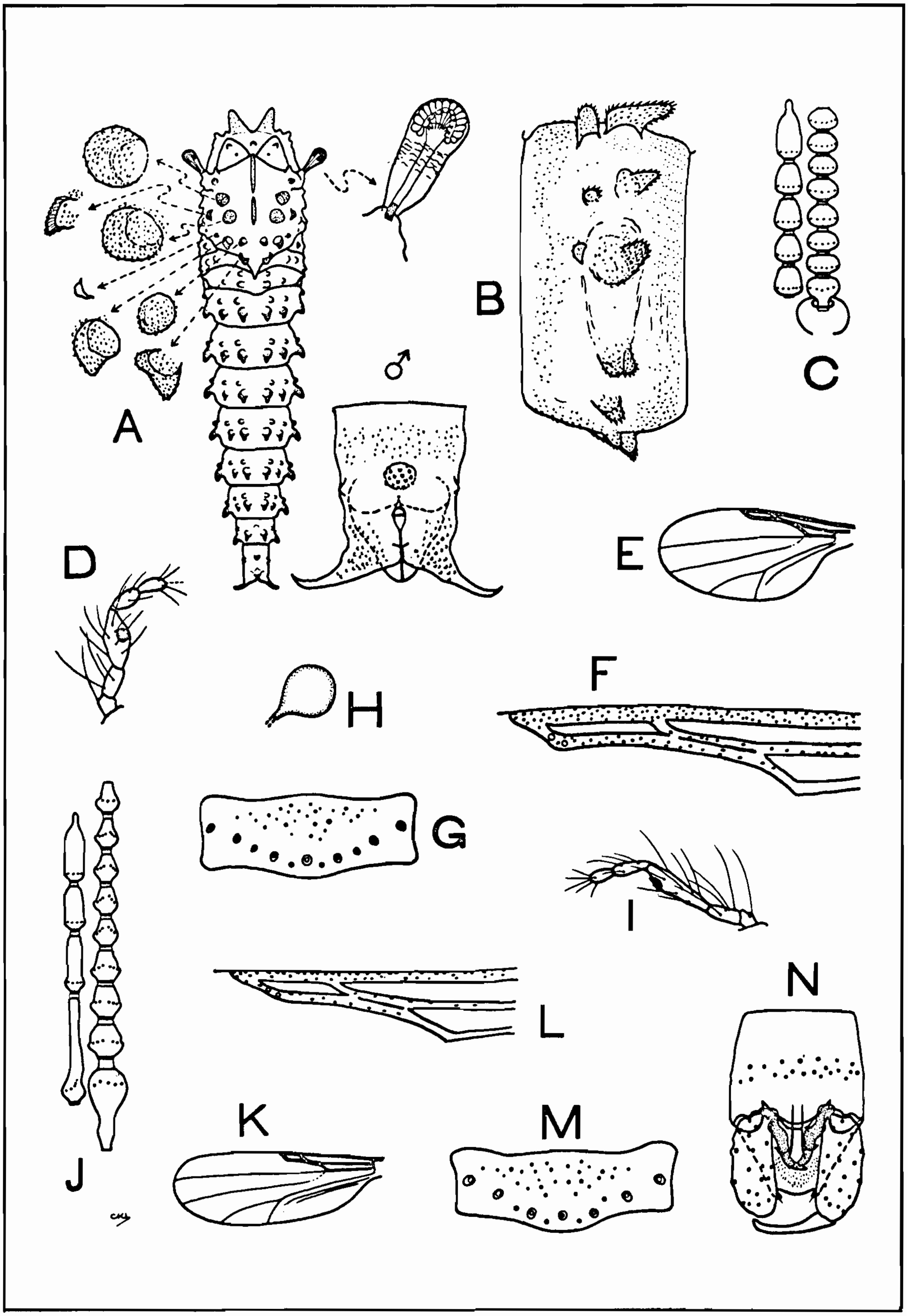
Thorax (Fig. 24A) bearing two anterior median ridges and nine pairs of tubercles, anteriormost two pairs closely associated with prothoracic horns. Prothoracic respiratory horn rather broad at apex and narrow at base, and bearing ten papillae in upper palisade and sixteen in lower palisade in male, and respectively eleven and fourteen in female; its length to width 2.11 in male and 2.15 in female; horn tracheal length to horn length 0.84 in male and 0.79 in female, and tracheal length to width in proportion of 9.60 in male and 7.33 in female.

Abdominal segment 1 with three pairs of low tubercles; segments 2-7 with four pairs of tubercles on dorsum (Fig. 24A, 24B); segments 3-7 similar in chaetotaxy (Fig. 24A, Fig.24B) with two pairs of dorsal tubercles, two pairs of lateral tubercles and two pairs of ventral

Fig. 24. Lasiohelea (Thyridomyia) gossympina n. sp.

- A-B, Pupa:
  - A, Pupa, dorsal view
  - B, Fourth abdominal segment
- C-H, Adult female:
  - C, Antenna
  - D, Maxillary palp
  - E, Wing
  - F, Anterior wing venation
  - G, Scutellum
  - H, Spermatheca
- I-N, Adult male:
  - I, Maxillary palp
  - J, Antenna
  - K, Wing
  - L, Anterior wing venation
  - M, Scutellum
  - N, Genitalia

Fig. 24



tubercles; segment 8 with two pairs dorsal tubercles, one pair of lateral and one pair of ventro-lateral and one pair of ventral tubercles. Terminal processes directed outwards, sharply pointed in both sexes. Male sexual processes ventral, short, rounded and united terminally (Fig. 24A).

Adult Female.-

Length 0.90 mm. Wing (24E) 0.60 x 0.32 mm.

Head with antennae and mouthparts brown; eyes and pedicels dark brown. Antennal segments (Fig. 24C) with segments 2-9 wider than long and segments 10-14 longer than wide, only last segment distinctly longer than the rest; AR 1.05. Maxillary palp (Fig. 24D) with segments in proportion of 5: 7: 14: 8: 6; PR 2.33; segment 3 bearing moderately large shallow sensory pit.

Thorax brown, scutellum (Fig. 24G) with nine strong bristles. Legs paler brown, with TR 2.83 in fore leg, 2.62 in middle leg and 2.73 in hind leg; hind tibial comb with seven tibial spines.

Wings brown; CR 0.54. Venation: vLR 1.19: 1: 2.58; rs/r_1 2.00: 1; first radial cell short, obliterated, second radial cell rather narrow, longer than first (1.37: 1); fmcu under end of r_1; m_{3+4}/cu_1 1.97: 1. Halteres brown.

Abdomen brown. Spermatheca (Fig. 24H) single, pyriform, with relatively long neck, measuring 41.40 x 37.95 μ and its duct 10.35 μ long.

Adult Male.-

Length 1.08 (1.02-1.16) mm. Wing (Fig. 24K) 0.71 (0.69-0.74) x 0.26 mm. Color as in female.

Antennae (Fig. 24J) relatively long with segments 2-9 flask-shaped and segments 10-14 elongate, segment 10 the longest; AR 0.91 (0.88-0.93).

Maxillary palp (Fig. 24I) slender, with segments in proportion of 4.5: 9.5: 17: 9: 6; segment 3 long, narrow, with shallow sensory pit bearing sessile sensilla just beyond slightly swollen portion; PR 3.40.

Thorax brown, with scutellum (Fig. 24M) bearing seven large bristles. Legs with TR 2.86 (2.85-2.88) in fore leg, 2.39 (2.31-2.50) in middle and 2.47 (2.38-2.67) in hind leg; hind tibial comb with 6-7 tibial spines.

Wings brown, CR 0.48 (0.47-0.49). Venation: vLR 1.15 (1.13-1.18): 1: 2.15 (2.12-2.20); rs/r_1 1.84 (1.83-1.85); first radial cell short, obliterated; second radial cell rather narrow, about as long as first (1.00 (0.89-1.06): 1) (Fig. 24L); fmcu under about tip of costa; m_{3+4}/cu_1 2.07 (1.91-2.24).

Genitalia (Fig. 24N): ninth sternite shorter than wide (0.76 (0.68-0.83): 1), ninth tergite about half as long as wide (0.57 (0.53-0.63: 1); parameres with basimeres about twice as long as wide (2.22 (2.15-2.30): 1) and telomeres 4.02 (3.56-4.50) times as long as wide, telomeres shorter than basimeres (0.80 (0.74-0.86): 1); aedeagus V-shaped, bipartite, each half curved and pointed at tip and bearing on inner side a slender vertical sclerite, slightly more than half as long as wide (0.60 (0.53-0.65): 1); claspettes M-shaped, very slender. b/c/b in proportion of 0.45 (0.40-0.50): 1: 0.45 (0.40-0.50).

<u>Holotype (Pupa)</u>.- Collected from decaying wood of rotting trunk of cotton tree at Wallace Way, Singapore in May 1962. Deposited in Lyman Entomological Museum, Macdonald College, Quebec.

<u>Paratypes</u>.- One female, three males and two associated pupal exuviae collected from the same habitat and locality, deposited in Department of Zoology, University of Singapore.

This species is close to Thyridomyia nodosa Saunders (1959) in structure of the male genitalia, especially in the bipartite nature of the aedeagus and the low claspettes, but differs from it in that the claspettes have a basal union and are more slender than those of nodosa. The ninth sternite is also different in being considerably longer. The pupa also resembles that of nodosa in its very spiny character, in the shape of the respiratory horn and in the larger anterior pair of tubercles on the median head sclerite, but is clearly different from nodosa in having more pairs of tubercles on the dorsum.

Because of the close similarities of pupal and adult characters between nodosa and gossympina it is reasonable to expect that the larva of the latter will be basically similar to those of nodosa, and it will bear rosette or "torch-like" setae on the body segments and possibly on the head as well.

C. Redescription of Lasiohelea (Thyridomyia) monilicornis (Coquillett) (1905)

Larva.-

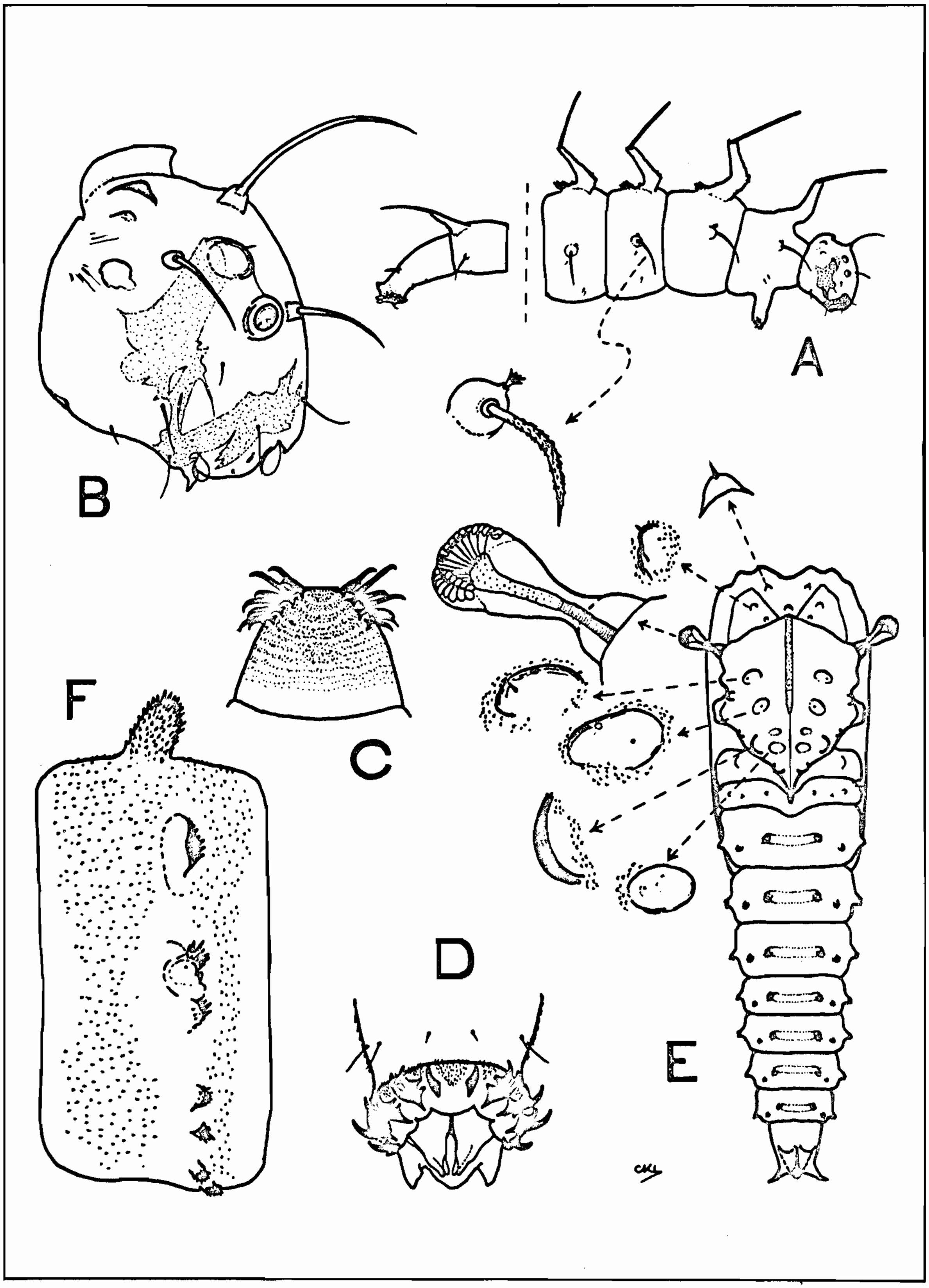
Length of full-grown fourth instar 2.25 mm. Color in life orange. Head dark brown with four pairs prominences on vertex and lateral markings; eyes with ocular setae; antennae and setae as in Fig. 25A; HR 1.27; OH/v 1.52; AR 0.44; qt/ts/sq 1.69: 1.69: 1: tt/antennae 0.28; qq/eyes 0.53; qq/ss 0.43.

Prothorax (Fig. 25A) with a setae borne on long tubercles, and ratio of length of filament to tubercle 1.20; a tubercles of prothorax and mesothorax nearly approximating at base, those of other segments separated but connected posteriorly by sclerotized band

Fig. 25. Lasiohelea (Thyridomyia) monilicornis (Goetghebuer)

A-D, Fourth-instar larva:
  A, Larva, lateral view
  B, Head
  C, Prothoracic pseudopod
  D, Anal pseudopod
E-F, Pupa:
  E, Pupa, dorsal view
  F, Fourth abdominal segment

Fig. 25



consisting of plate-like sclerotizations. Chaetotaxy on pro- and mesothorax similar, each with the normal large a and b setae and two pairs of minute setae as figured (Fig. 25A). Prothoracic pseudopod (Fig. 25C) with five anterior and four posterior pairs of hooklets with length, width and depth in proportion of 1.77: 1.47: 1; Metathorax with two pairs of minute setae, one pair just ventral to b setae and the other near mid-ventral surface, as in Fig. 25A.

Chaetotaxy on abdominal segments 1-7 similar, with three pairs of minute setae as figured. Postèrior pseudopod (Fig. 25D) with usual nine pairs of hooklets arranged in two rows. Anal blood gills two, bilobed.

Cuticular armature scale-like, more prominent on pleura and ventral surface.

Pupa.-

Length 1.49 mm. in female and 1.50 mm. in male. Color as in larva but dark just prior to adult emergence.

Median head sclerite with three tubercles, anterior pair setigerous; lateral sclerites with two small tubercles each (Fig. 25E). Ratio of head length to thorax length 0.46 in ventral aspect and 0.23 in dorsal aspect in female and respectively 0.49 and 0.25 in male.

Thorax bearing a median anterior prominence and eight pairs of tubercles on dorsum (Fig. 25E). Prothoracic horn narrow apically, broad distally, 1.63 and 2.27 times longer than its greatest width in female and male respectively and bearing spiracular papillae in two palisades, 13 in upper and 18 in lower in female, and 15 in upper and 18 in lower in male; tracheal length to horn length 6.67 and 9.67 respectively in female and male.

Chaetotaxy on abdominal segments 2-7 similar (Fig. 25E) with two pairs dorsal tubercles, one composite lateral tubercle consisting of two adjoining tubercles, and four pairs ventral tubercles (Fig. 25F). First abdominal segment with four pairs of tubercles on dorsum (Fig. 25E).

Cuticular armature finely shagreened (Fig. 25F).

Adult Female.-

Length 1.47 mm. Wings (Fig. 26D) 0.89 mm. by 0.41 mm.

Head with antennae and mouthparts dark brown and eyes black. Clypeus with 10 bristles (Fig. 26B). Maxillary palp (Fig. 26C) distinctly five-segmented, with third segment rather short and slender and bearing scattered sensilla on inner edge; last segment short, connected to preceding segment by rather wide membranous joint; PR 3.17. Antenna (Fig. 26A) dark brown with AR 0.87.

Thorax dark brown with scutellar arrangement as shown (Fig. 26F). Legs uniformly brown, TR 2.35 in fore leg, 2.47 in middle leg and 2.61 (2.59-2.62) in hind leg; claws and empodium normal; apical tibial comb with eight bristles.

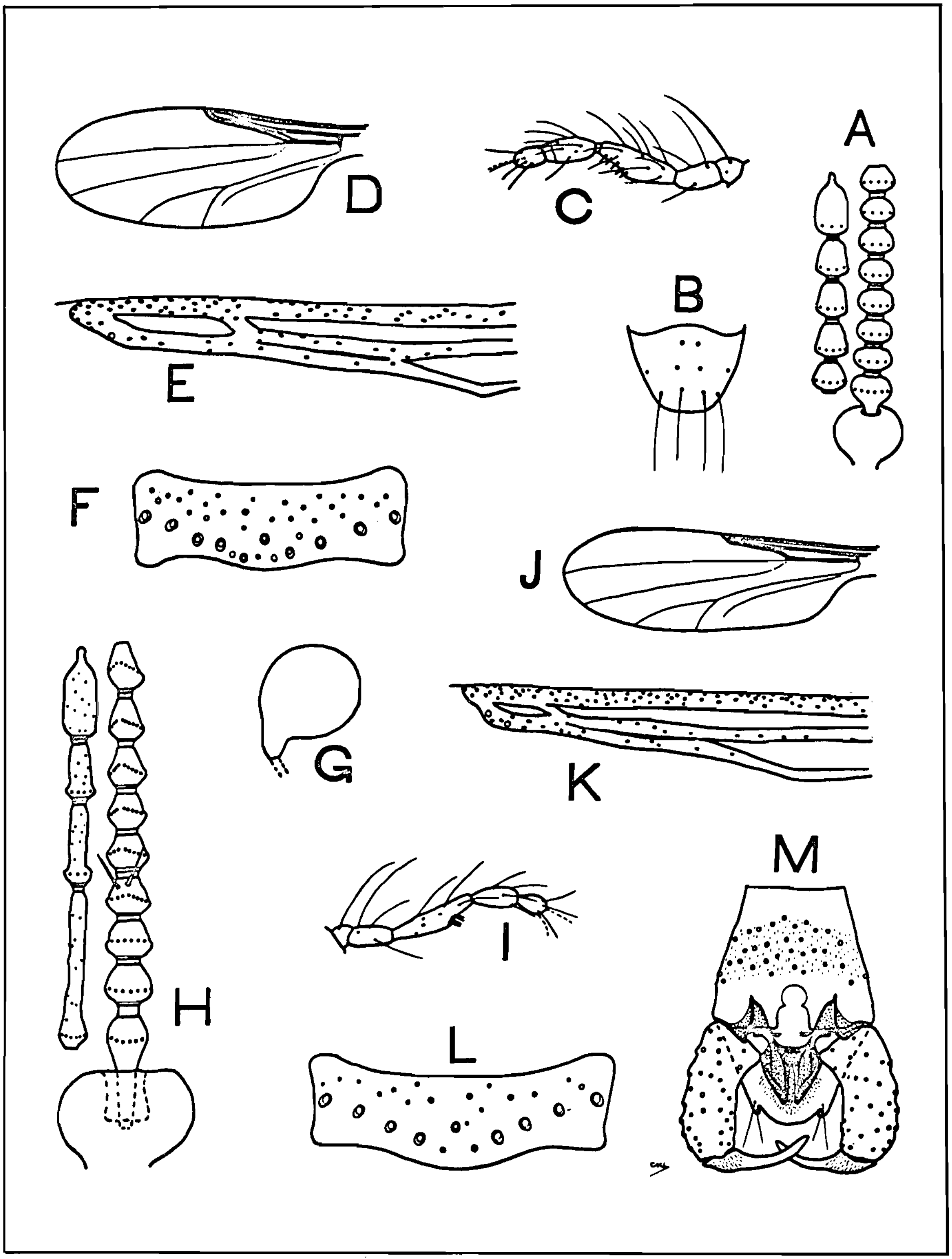
Wings dark brown; CR 0.50 (0.50-0.51). Venation: vLR 1.41 (1.40-1.42): 1: 2.67; rs/r_1 1.66 (1.66-1.68); first radial cell (Fig. 26E) practically obliterated, second radial cell small, slightly shorter than first; RR 0.82 (0.78-0.87); fmcu under about middle of first radial cell; m_{3+4}/cu_1 1.84 (1.77-1.92). Halteres light brown.

Abdomen with cerci brown; spermatheca (Fig. 26G) single, large, 79.35 μ long by 69.00 μ wide, and with neck bent, measuring 17.25 μ long.

Fig. 26. *Lasiohelea* (*Thyridomyia*) *monilicornis* (Goetghebuer)

A-G, Adult female:
  A, Antenna
  B, Clypeus
  C, Maxillary palp
  D, Wing
  E, Anterior wing venation
  F, Scutellum
  G, Spermatheca
H-M, Adult male:
  H, Antenna
  I, Maxillary palp
  J, Wing
  K, Anterior wing venation
  L, Scutellum
  M, Genitalia

Fig. 26



Adult Male.-

Length 1.54 (1.50-1.58) mm. Wings (Fig. 26J) 0.94 (o.87-1.01) mm. by 0.32 (0.28-0.36) mm.

Head with antennal filament and mouthparts brown and eyes and pedicels dark brown to black. Maxillary palp (Fig. 26I) slender, with third segment narrow and bearing sensilla in a group, practically in a sensorium; PR 4. Antenna (Fig. 26H) light brown, with pedicel dark brown to black; AR 0.96 (0.95-0.96).

Thorax dark brown; scutellum (Fig. 26L) with bristle arrangement as shown. Legs uniformly brown; TR 2.57 (2.46-2.69) in fore leg, 2.39 (2.36-2.42) in middle leg and 2.49 (2.40-2.58) in hind leg; claws slender, empodia normal; apical tibial comb with eight bristles.

Wings (Fig. 26J) brown; CR 0.46 (0.45-0.47). Venation: vLR 1.30 (1.24-1.37): 1: 2.55 (2.21-2.90); rs/r_1 1.43 (1.36-1.50); first radial cell practically obliterated, second radial cell narrow and very short, not exceeding half length of first; RR 0.42 (0.40-0.43); fmcu under just beyond tip of second radial cell; m_{3+4}/cu_1 1.90 (1.86-1.93). Haltere light brown.

Abdomen brown. Genitalia (Fig. 26M): sternite 9 bearing moorish window, about as long as wide (0.99: 1), and tergite 9 about half as long as wide (0.48: 1). Parameres with basimeres curved at basal third, about $2\frac{1}{2}$ times as long as wide (2.59: 1), and with telomere slightly shorter than basimere (0.89: 1) and about $5\frac{1}{2}$ times as long as greatest width at base (5.68: 1). Claspettes typical of subgenus, with basal arms triangular, broad at base and narrow apically, and with processes also triangular, with tips facing medially. Aedeagus shield-shaped, with narrow, curved, basal arms pointing horizontally and two vertical sclerotized medial thickenings, the whole appearing essentially bipartite.

Syntypes.-

Early stages were collected from moss growing on soil at Morgan Aboretum, Macdonald College, throughout the summer of 1964. Adults were obtained from rearings of the early stages. 2 larvae, 12 pupae, 3 males, 1 female and 11 asociated pupal exuviae in personal collections.

Other species.-

Species described in all stages include:

Thyridomyia palustris Saunders (1925); Parasitology *17*: 269

Forcipomyia (Thyridomyia) aspinosa Saunders (1956); Can. J.Zool.
34: 692

Forcipomyia (Thyridomyia) nodosa Saunders (1959); Can. J. Zool.
37: 43

Species attributable to this subgenus on male genitalic characters include:

Ceratopogon frutetorum Winnertz (1852); Linn. Ent. *6*: 1-80

Forcipomyia aethiopiae Ingram and Macfie (1924); Ann. Trop.
Med. parasitol. *18*: 582

Forcipomyia kitasirakawae Tokunaga (1940); Tenthredo *3*: 94

Lasiohelea esakii Tokunaga (1940); Tenthredo *3*(2): 169

Forcipomyia (Thyridomyia) hamata Tokunaga (1959); Insects of
Micronesia *12*(3): 207

Lasiohelea skiaphila Clastrier (1960); Arch. Inst. Pasteur
Afrique du Nord *38*: 522

Lasiohelea nana Macfie (1944); Bull. Entomol. Res. *35*: 297

5. NEW SUBGENUS (LANE'S LASIOHELEA STYLIFER LUTZ)

Subgenus type stylifer Lutz (1913)

Centrorhynchus stylifer Lutz (1913), Mem. Inst. Osw. Cruz. 5:63

Lasiohelea stylifer Lane (1947), Arq. Fac. Hig. Saude Publ. Univ. Sao Paolo 1: 161

Lasiohelea stylifer Ortiz (1952), Rev. Sam. Assist. Soc. 17: 242

DIAGNOSIS

Larva.-

Length of full-grown fourth instar about 4 mm. Body elongate, spiny, a hairs short; several other dark setae. Head hypognathous, distinct, brown, with a reticulate design on posterior portion. q, t and s setae simple, smooth, thin; antennae short, hyaline at apex. Prothoracic pseudopod undivided, bearing two rows of curved hooklets, 12 hooklets in each row; anterior row hyaline, posterior row strongly sclerotized. Posterior pseudopod bearing a considerable number of hooklets, 50-60 around the anus in a double ring, all curved and heavily sclerotized. Abdominal segments bearing rows of irregular bristles on ventral surface.

Pupa.-

Prothoracic horn small, short, boot-shaped, bearing a row of more than 20 irregular spiracular papillae winding across the extremity. Cephalothorax with anterior and dorsal tubercles elongate, spiny and bearing pointed setae, and other tubercles elongate, rugose and pointed at apex, with small apical setae in some. Abdomen spiny with dorso-marginal tubercles forming protuberances bearing thin setae. Larval exuviae retained in last abdominal segment.

Adult Female.-

Body length about 1.6 mm. Wings about 1.00 mm. by 0.4 mm.

Head black, with eyes contiguous. Antennae with segments 2-9 short, segments 3 and 4 as wide as long, 5-8 a little longer than wide and segments 10-14 long; AR about 1.8. Maxillary palp distinctly five-segmented, with segment 3 dilated, fusiform and tapered distally beyond circular sensorium, and with segment 4 more than half length of third; PR about 2.6.

Thorax with scutellum bearing 8 small bristles in anterior row and 9 large bristles in posterior row. Legs with TR about 2.2 in fore leg, 2.0 in middle and 2.1 in hind leg. Wing with first radial cell obliterated, second radial cell elongated and narrow; CR about 0.6.

Spermatheca single, large, with hyaline duct.

Adult Male.-

Unknown.

6. SUBGENUS DACNOFORCIPOMYIA CHAN AND SAUNDERS (1965)

Subgenus type anabaenae Chan and Saunders (1965)

DIAGNOSIS

Larva.-

Slender, with small head on long neck. Head hypoghathous, with one pair small, sharp, forward-pointed prominences on vertex; antennae short, stout, on low socle; q hairs prominent, curved, simple; s hairs simple; t hairs short, straight, simple; occular setae absent. Prothoracic pseudopod long, armed distally with two stout black hooklets. a and b hairs of body segments slender, finely setulose, on long tubercles; last abdominal segment with one pair small dorsal horns; ventral surface of most abdominal segments divided into creeping ridges. Anal pseudopod with only six stout, black hooklets. Cauda absent.

Pupa.-

Head, thorax, and abdomen with only small tubercles, some setigerous. Prothoracic respiratory horn small straight-sided, with narrowed base forming slight posterior heel; respiratory papillae in row across rounded tip. Last abdominal segment with sharp lateral hooks retaining larval exuviae; male sexual processes ventral.

Adult Female.-

Antennae with basal flagellar segments globular, first five somewhat compressed, all bearing pair of hyaline setae moderately short; AR 2.2. Maxillary palps short, third segment broad without distal neck, bearing circular sensorium containing sessile[1] sensilla; fourth and fifth segments distinct. TR of hind leg about 1.9. Wing with first radial cell closed, second radial cell practically closed; CR 0.6. One spermatheca..

Adult Male.-

Antennae with basal flagellar segments globular to flask-shape, distal four segments elongate, AR about 1.2. Maxillary palps short, slender, segment 3 only slightly swollen, with shallow circular sensorium containing sessile sensilla. Wings with both radial cells closed; CR about 0.54. Claws with normal empodium. Hypopygium with ninth sternite shorter than wide; parameres with basimeres

[1] "sessile" - term denotes "stalkless"

about twice as long as wide and telomeres straight, untapered, equal in length to basimeres; claspettes a high slender arch with delicate anterior flange; aedeagus bipartite, each half with median rounded lobe, straight anterior arm, bluntly rounded posterior tip; joined by fine chitinous filament to base of basimere. (This diagnosis is preliminary and will be revised when all stages of more species are discovered).

Species described in all stages.-

Forcipomyia (Dacnoforcipomyia) anabaenae Chan and Saunders (1965); Can. J. Zool. 43: 528

Other Species.-

There is a possibility that the following blood-sucking species which was recorded from Borneo belongs to Dacnoforcipomyia but its systematic position is uncertain (Johannsen, 1932).

Ceratopogon agas Rondani (1875); Ann. Mus. Genova 7: 462

7. SUBGENUS LASIOHELEA KIEFFER (1921)

Subgenus type pilosipennis Kieffer (1921)

DIAGNOSIS

Larva.-

Orange-brown, rarely yellow, slender. Head dark, relatively small, hypognathous, with four low prominences on vertex; antennae small, normal in form and position; q and s hairs pectinate or simple; ocular setae present. a and b hairs torch-like, variable in length in tubercle and filament; dorsum of last segment and sometimes of penultimate segment, with paired horn-like tubercles or rudiments of same. Prothoracic pseudopod well-developed, undivided, with four pairs stout black hooklets and five pairs slender, hyaline ones. Anal pseudopod bearing an almost complete double ring of nine pairs of hooklets. Cauda replaced by low, rounded tubercles across tip of last segment. Cuticular armature scale-like.

Pupa.-

Orange or yellow. Exuviae faintly pigmented. Head with three small tubercles, anterior pair setigerous, on median sclerite, and one small tubercle on each lateral sclerite. Thorax and abdomen with many tubercles, mainly small, non-setigerous or with short setae. Terminal processes directed outwards, sharply pointed; male sexual processes ventral. Prothoracic horns narrow, with usually distinct posterior 'heel' and with 4-14 spiracular papillae across distal end.

Adult Female.-

Antennae with basal segments discoidal, subspherical or short-oval, without neck parts; distal five segments cylindrical and distinctly elongate; AR large, 1.5-3.2. Maxillary palp distinctly five-segmented, segment 3 usually stout, with sensorium or scattered sensilla. Hind TR usually larger than 2.0 and less than 3.0; empodia and claws normal. Wing unadorned, with dense macrotrichia, lying less closely than in Forcipomyia (Forcipomyia); bare areas along veins distinct; costa extending distinctly beyond middle of wing (CR 0.56-0.74); first radial cell slit-like or obliterated, second radial cell usually far longer than first. One spermatheca.

Adult Male.-

TR of hind leg somewhat smaller than in female. Male hypopygium with telomeres somewhat thickened apically or preapically; claspettes slender, with basal arms and basal union forming an arch, posterior extension of basal arms present in only one species (cornuta Saunders, 1964); aedeagus complicated, often bipartite, and usually with hook-like processes at apex.

Lasiohelea (Lasiohelea) propria CHAN NEW SPECIES

Larva.-

Length of full-grown fourth instar larva 2.88 mm. Color in life orange to pink.

Head dark brown; eyes, antennae and setae as in Fig. 27A. HR 1.48; OH/v 2.05; AR 2.75; qt/ts/sq 1.80: 1. 87: 1; tt/ant 0.47; qq/eyes 0.39; qq/ss 0.33.

Prothorax (Fig. 27B) with torch-like a and b setae, their lengths of filament and tubercle in proportion of 1.41: 1 and 1.78: 1 respectively; prothoracic pseudopod (Fig. 27B, 27C) with length, width and depth in proportion of 1.40: 1.55: 1. Chaetotaxy similar in thoracic segments (Fig. 27B) but metathoracic a setae located closer to each other dorsally than their position in other segments.

Abdominal chaetotaxy similar in segments 2-7 (Fig. 27D), with a and b setae torch-like, that on segments 8 and 9 as in Figs. 27E and 27F respectively, Posterior pseudopod typical of subgenus, with eight pairs of black curved hooks.

Cuticular armature scale-like (Fig. 27B, 27D, 27E, 27F), more prominently seen on ventral surface and pleura.

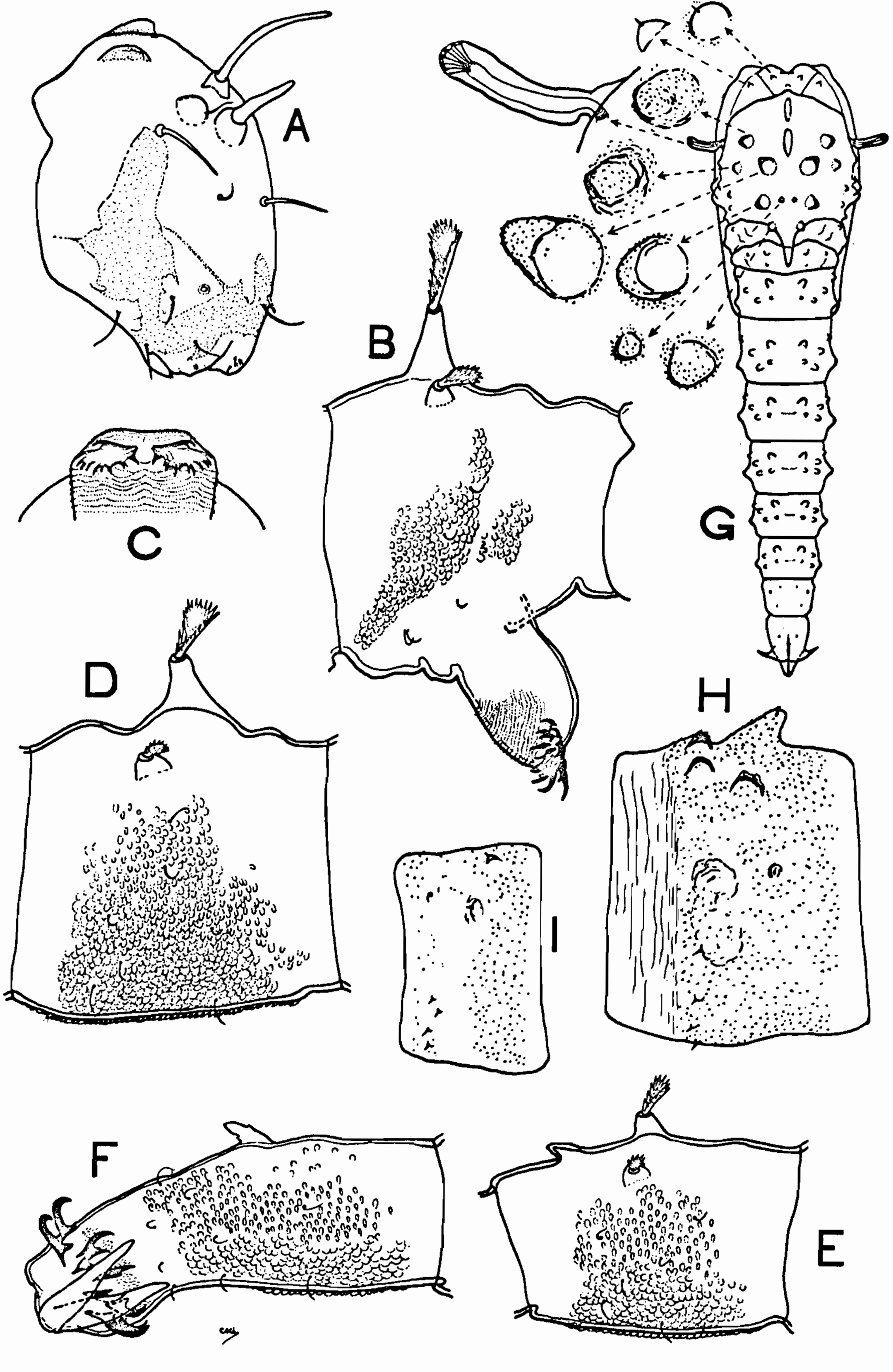
Pupa (Male).-

Length 2.04 mm. Color as in larva but dark just prior to

Fig. 27. Lasiohelea (Lasiohelea) propria n. sp.

- A-F, Fourth-instar larva:
  - A, Head
  - B, Prothorax and neck
  - C, Prothoracic pseudopod
  - D, Second abdominal segment
  - E, Penultimate segment
  - F, Last segment
- G-I, Pupa:
  - G, Pupa, dorsal view
  - H, Fifth abdominal segment
  - I, Eigth abdominal segment

Fig. 27



emergence of adult.

Median head sclerite with three tubercles, anterior pair spiniferous; lateral sclerites with one tubercle each, also spiniferous (Fig. 27G); cephalothorax about twice as long as greatest width (1.85: 1). Ratio of length of head to thorax 0.40 in ventral aspect and 0.23 in dorsal aspect.

Thorax bearing on dorsum two median prominences and seven pairs of tubercles, anteriormost pair setigerous (Fig. 27G). Prothoracic horn (Fig. 27G) narrow, with posterior heel distinct, 4.25 times longer than its greatest width; tracheal length to horn length 0.79: 1, and bearing at apex 7-8 spiracular papillae.

Chaetotaxy on abdominal segments 3-7 similar. Segments 2-7 with four pairs of tubercles on dorsum (Fig. 27G); segment 8 with three pairs and segment 9 with one pair. Lateral and ventral tubercles minute, setigerous, as shown in Fig. 27H and 27I.

Cuticular armature finely shagreened.

Adult Female.-

Length 1.20 mm. Wing (Fig. 28D) 0.82 x 0.38 mm.

Head with antennae and mouthparts dark brown, eyes black; clypeus with 26 bristles (Fig. 28B). Maxillary palp (Fig. 28C) rather stout, with third segment stout and bearing large, shallow sensory pit; last segment narrow, slightly shorter than third (0.77: 1); PR 1.65. Antenna (Fig. 28A) dark brown, pedicel darker brown; AR 1.69.

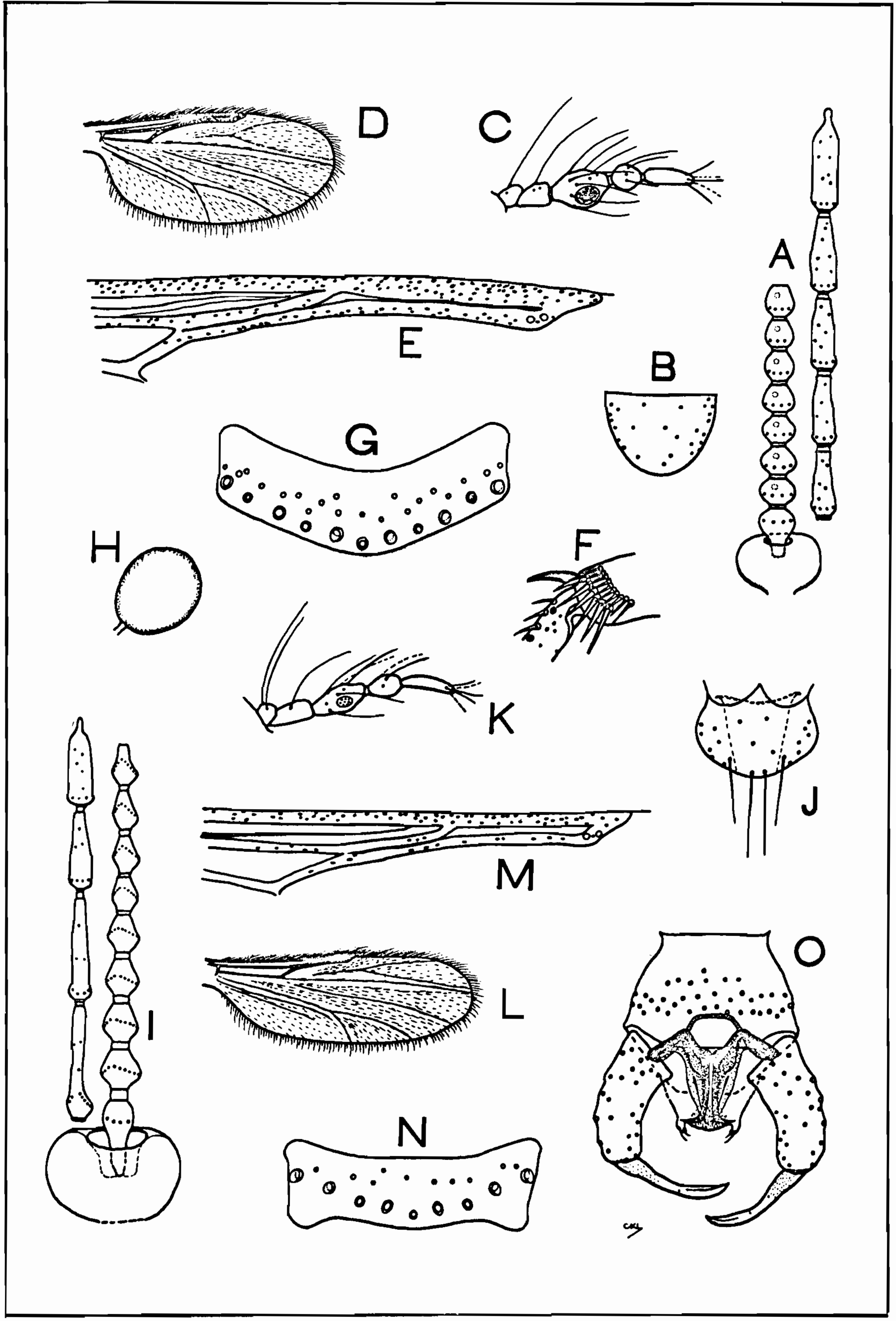
Thorax dark brown, with scutellar bristle arrangement as shown (Fig. 28G). Legs uniformly dark brown; fore TR 2.50; mid TR 1.94 and hind TR 2.10; claws and empodia normal; apical tibial comb with

Fig. 28. _Lasiohelea (Lasiohelea) propria_ n. sp.

A-H, Adult female:
- A, Antenna
- B, Clypeus
- C, Maxillary palp
- D, Wing
- E, Anterior wing venation
- F, Hind tibial comb
- G, Scutellum
- H, Spermatheca

I-O, Adult male:
- I, Antenna
- J, Clypeus
- K, Maxillary palp
- L, Wing
- M, Anterior wing venation
- N, Scutellum
- O, Genitalia

Fig. 28



seven bristles (Fig. 28F).

Wings dark brown; CR 0.62. Venation: vLR 1.18: 1: 2.12; rs/r_1 3.17; first radial cell (Fig. 28E) slit-like, second radial cell except for proximal end also slit-like, longer than first; RR 1.79; fmcu under end of first radial cell; m_{3+4}/cu_1 1.93. Haltere light brown with knob white.

Abdomen with cerci brown; spermatheca (Fig. 28H) single, large, subspherical, with narrow duct, and measuring 69 x 53.48 μ.

Adult Male.-

Length 1.47 mm. Wings 0.90 x 0.31 mm.

Head with antennae and mouthparts brown, eyes and pedicels dark brown to black; clypeus with 21 bristles (Fig. 28J). Maxillary palp (Fig. 28K) rather slender and long, with third segment moderately narrow, slightly longer than last segment (1.06: 1), and bearing at about middle a shallow, rather small sensory pit; PR 1.97. Antenna (Fig. 28I) brown, with pedicel dark brown; AR 0.96.

Thorax dark brown; scutellum with bristle arrangement as shown (Fig. 28N). Legs uniformly brown; fore TR 2.20; mid TR 1.81; hind TR 1.88; claws slender, empodia normal; apical tibial comb with 7-8 bristles.

Wing (Fig. 28L) brown; CR 0.56. Venation: vLR 1.18: 1: 1.89; rs/r_1 2.28; first radial cell slit-like, second radial cell narrow, more than $1\frac{1}{2}$ times longer than first (1.85: 1) (Fig. 28M); fmcu under about middle of second radial cell; m_{3+4}/cu_1 2.38. Haltere brown with knob white.

Abdomen brown. Genitalia (Fig. 28 O): sternite 9 slightly more than half as long as wide (0.61: 1), and tergite 9 about $\frac{1}{4}$ as long as wide (0.27: 1). Parameres with basimere widest at base and narrowest at tip, 2.84 times as long as greatest width, and with telomere shorter than basimere (0.87: 1), pointed and curved at tip and slightly constricted at middle. Claspettes arch-like, with basal arms and basal union slender, b/c/b in proportion of 1.28: 1: 1.28. Aedeagus V-shaped, bipartite, with basal arms, basal arch, mesal edges and outward-turning tips heavily sclerotized; caudo-lateral shoulders or lateral edges slightly sclerotized.

Holotype (fourth instar larva).-

Collected in March 1962, on algae growing on leaves of a moss growing on rocks on the bank of a fast flowing stream in a forest in Gunong Pulai, Johore, Malaya. Deposited in Lyman Entomological Museum, Macdonald College, Quebec, Canada.

Paratypes.-

Collected from same habitat and locality as holotype; 2 larvae, 2 males, 5 females and 2 associated pupal exuviae, deposited in the Department of Zoology, University of Singapore.

This species is close to Lasiohelea longicornis Tokunaga (1940) from Honshu and Ryukyu Is, Japan, in male genitalic structures, especially in the bipartite aedeagus with outward-turning tips and the low arch of the claspettes whose basal arms arise from the same place as those of the aedeagus. This species however differs from longicornis in the less rounded top of the claspette arch and in the absence of the rounded swellings of the aedeagus on the outer surface. It also differs from longicornis, among other characters, in the smaller

PR of 1.97 against 3.7 of longicornis and in the tarsal ratios: 2.20 in fore leg, 1.81 in mid leg, and 1.88 in hind leg against longicornis' 1.81, 1.53 and 1.28 respectively.

When the early stages of longicornis are discovered comparisons with those of this new species will certainly amplify the differences that separate these two species.

Lasiohelea (Lasiohelea) uncuspromissa CHAN NEW SPECIES

Larva.-

Length of third instar larva (Fig. 29A) 2.68 mm. Color in life orange-red, head brown and tubercles of setae white.

Head typically small, hypognathous, with two prominences on vertex; eyes with ocular setae; antennae and setae as in Fig. 29B. HR 1.33; OH/v 1.53; AR 1.77; qt/ts/sq 1.44: 1.40: 1; tt/ant 0.51; qq/eyes 0.46; qq/ss 0.39.

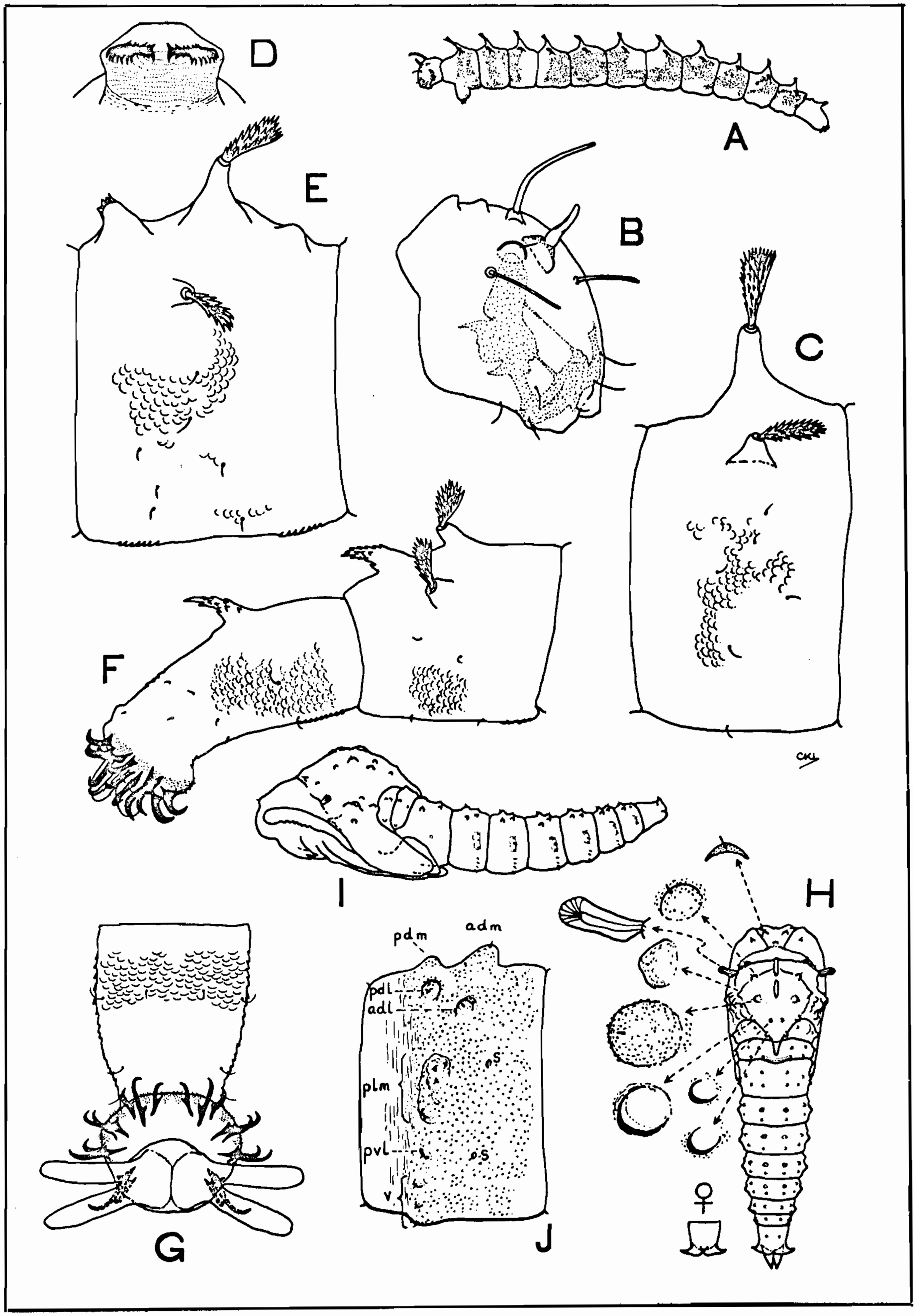
Thorax bears on each segment torch-like a and b setae with six pairs of minute setae (Fig. 29C); prothoracic a and b setae with filament and tubercle in proportion of 1.22: 1 and 1.67: 1 respectively; prothoracic pseudopod (Fig. 29D) bearing twenty-two hooks and with length, width and depth in proportion of 1.31: 1.26: 1.

Abdominal chaetotaxy similar in segments 1-7 with ten pairs of tubercles, setae a and b and c large, the rest minute (Fig. 29E). Segments 8 and 9 with chaetotaxy as shown in Fig. 29F; both with paired horn-like tubercles on dorsum. Anal pseudopod (Fig. 29G) with two rows of slender, curved hooks (anterior row of five shorter pairs and posterior row of four longer pairs), and two bilobed anal blood gills.

Fig. 29. *Lasiohelea* (*Lasiohelea*) *uncuspromissa* n. sp.

- A-G, Fourth-instar larva:
  - A, Larva, lateral view
  - B, Head
  - C, Metathoracic segment
  - D, Prothoracic pseudopod
  - E, Third abdominal segment
  - F, Last two segments
  - G, Anal pseudopod
- H-J, Pupa:
  - H, Pupa, dorsal view
  - I, Pupa, lateral view
  - J, Sixth abdominal segment

Fig. 29



Cuticular armature scale-like.

Pupa (Female).-

Length 1.84 mm. Color orange-red, darker red in thorax.

Median head sclerite with three tubercles, the anterior pair (antero-marginal) setulose; lateral sclerites each with a setulose tubercle (antero-dorsal). On postero-ventral head region, both ventro-median and ventro-lateral tubercles present, the former setate, the latter an elongated, indistinct marking. Cephalothorax 1.76 times as long as its width. Ratio of length of head to thorax 0.41 in ventral aspect and 0.24 in dorsal aspect.

Thorax (Fig. 29H) bearing two median ridges and eight pairs of low tubercles of which two pairs are anterior to prothoracic horn. Of the remaining six pairs on dorsum, the anteriormost three pairs bear minute setae, the posterior three pairs non-setate. Prothoracic horn (Fig. 29H) club-shaped, with about eight spiracular papillae across tip, its length 2.80 times its width and the ratio of tracheal length to horn length 0.74.

Abdominal segments 1-6 each bearing four pairs of small tubercles on dorsum (Fig. 29H, 29J). Segment 1 has, in addition, a pair of lateral tubercles bearing minute setae. Segments 3-6 similar in chaetotaxy, each bearing in addition to above-mentioned, four pairs of tubercles, three pairs of posterior latero-marginal tubercles (p.l.m.), one pair of posterior ventro-lateral tubercle (p.v.l.) and three pairs of ventral tubercles (v) (Fig. 29J). Terminal processes directed outwards, sharply pointed, retaining larval exuviae on last three abdominal segments. Male sexual processes ventral, short.

Adult Female.-

Length 1.31 mm. Wings 0.77 x 0.35 mm.

Head dark brown, with mouthparts brown; eyes almost contiguous dorsally; clypeus (Fig. 30B) with 13 setae. Maxillary palp (Fig. 30C) stout, somewhat ovoid and bearing very large, oval, shallow sensory pit; PR 1.50; five segments in proportion of 4: 8: 13: 7: 9. Antennae (Fig. 30A) with pedicel dark brown, other segments uniformly lighter brown; basal flagellar segments short, subspherical to oval, segment 3 wider than long, segment 4 as wide as long, segments 5-9 slightly longer than wide; AR 1.77; segments 2-14 in proportion of 9.5: 6: 6.5: 7: 7: 7: 7: 8:20: 21: 23: 23: 30.

Thorax entirely brown, with scutellum (Fig. 30F) bearing six large bristles. Legs entirely brown; tibial comb with 6-7 anterior large spines and 10-12 posterior small spines; claws and empodia slender (Fig. 30G); TR 2.50 in fore leg, 2.25 in mid leg and 2.11 in hind leg; leg segments except for basal two, in proportion of 81: 87: 50: 20: 15: 12: 11 in fore leg, 98: 107: 49.5: 22: 17.5: 13: 11 in middle leg and 99: 103.5: 64: 28: 22: 17: 11 in hind leg.

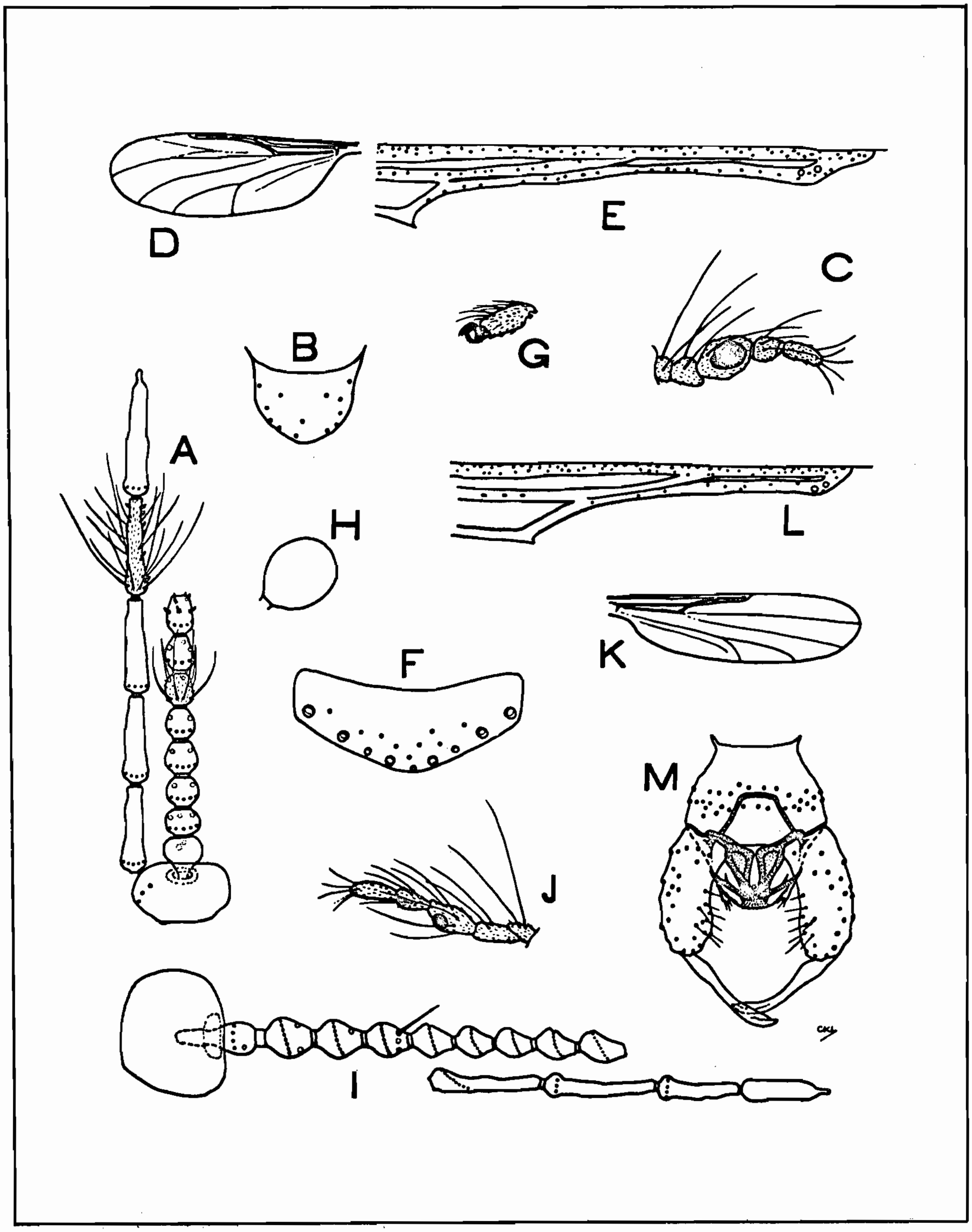
Wing (Fig. 30D) brown, costa and radius darker brown, bearing thick long hairs; bare areas along veins distinct in proximal two-thirds, indistinct in distal third; CR 0.66. Venation: rs/r_1 2.25; rs longer than r (1.36: 1); first radial cell obliterated, second radial cell long, very narrow, longer than first (1.31: 1) (Fig. 30E); mcu/r 1.53: 1; fmcu under about end of first radial cell. Halteres brown, with knobs white.

Abdomen, including cerci, brown; spermatheca (Fig. 30H) single,

Fig. 30. Lasiohelea (Lasiohelea) uncuspromissa n. sp.

A-H, Adult female:
  A, Antenna
  B, Clypeus
  C, Maxillary palp
  D, Wing
  E, Anterior wing venation
  F, Scutellum
  G, Last segment of hind leg
  H, Spermatheca
I-M, Adult male:
  I, Antenna
  J, Maxillary palp
  K, Wing
  L, Anterior wing venation
  M, Genitalia

Fig. 30



large, short oval, 62.07 x 51.72 μ.

Adult Male.-

Length 1.45 mm. Wing 0.84 x 0.26 mm. Color as in female.

Head with vertex dark brown, fronto-clypeus and mouthparts lighter brown; eyes contiguous above; clypeus with 13 setae; proboscis about two-thirds as long as head capsule (0.66:1). Maxillary palp (Fig. 30J) more slender than that of female, with five segments in proportion of 4: 6: 10:6.5: 9; segment 3 with shallow depression containing a group of sensillae; PR 1.88 (1.82-2.00). Antenna (Fig.30I) with scape and pedicel dark brown, other segments lighter brown; AR 0.96 (0.93-0.99); segments 2-14 in proportion of 16: 10: 10: 9.5: 9.5:8: 8: 9: 9: 22.5: 23: 18: 21.

Thorax entirely brown. Scutellum with six strong bristles along caudal margin. Legs entirely brown; tibial comb of hind leg with seven anterior large and 10-11 posterior small bristles; claws rather small, slender and curved; empodium thin and slender; leg segments except basal two, in proportion of 90: 99: 57: 28: 2.15: 14: 10 in hind leg, 98: 107: 47: 24.5: 17.5: 12: 11 in middle leg, and 92: 85: 50: 22: 17: 12: 10.5 in fore leg. TR 2.27 in fore leg, 1.88 in middle leg and 2.03 in hind leg.

Wing (Fig. 30K) with veins brown, bare areas along veins distinct. CR 0.59. Venation: vLR 1.17: 1: 1.79; rs/r_1 2.40; rs/r 0.86; first radial cell obliterated, second radial cell very narrow, slightly longer than first (1.15: 1); m_{3+4}/cu_1 2.59; fmcu under about middle of second radial cell; mcu/r 1.54. Halteres with knobs white.

Abdomen with sclerites brown, membranes pale. Genitalia (Fig.30M) sternite 9 rather short and broad, shorter than wide (0.83: 1); tergite 9 about as long as wide (1.03: 1), somewhat round on lateral and caudal margins. Parameres with basimeres cylindrical, about three times as long as wide (2.73: 1) and with telomeres slender, little shorter than basimeres (0.83: 1), narrowed at middle and curved inwards at tip. Claspettes arch-like, slender; basal arms and basal union in proportion of 1.64: 1: 1.64. Aedeagus bipartite, distal ends of each half with long, hook-like,outwardly-directed sclerites; median portion triangular, strongly sclerotized around borders.

Holotype (Adult Male).- Reared from larvae collected from mosses, liverworts and algae growing on clay bank at Wallace Way, Singapore, in June 1961.

Paratypes.- Collected from same habitat and locality as holotype; 3 larvae, 4 females, 2 males and 5 associated pupal exuviae, deposited in the Department of Zoology, University of Singapore.

This species is distinct from recorded species but somewhat resembles Lasiohelea carolinensis Tokunaga (1940) from Micronesia in structure of the aedeagus of the male, especially in the long outward-turning hooks. It differs from carolinensis in the much taller arch-like claspettes in the male.

It differs from Lasiohelea villosa Macfie (1934) from Selangor, Malaya (in which only the female is known) in its much smaller size (0.77 mm. to 1.7 mm. in wing length), higher hind TR (2.1 to 1.8-1.9) and in the third palpal segment which bears a large sensory pit instead of "without pit but bearing numerous sensory hairs on a large depressed area about middle"(Macfie, 1934).

Other Species.-

Species described in all stages are:-

attenuata (Saunders) (1964); Can.J.Zool. 42: 469

atratula (Goetghbuer) (1935); Rev. Zool. Bot. Afr. 27: 149

cornuta (Saunders) (1964); Can. J.Zool. 42: 464

flavescens (Saunders) (1964); Can. J.Zool. 42: 471

fairfaxensis (Wirth) (1951); Proc. Entomol. Soc.Wash. 53(6): 317

intermedia (Saunders) (1964); Can. J.Zool. 42: 468

longineura (Saunders) (1964); Can. J. Zool. 42: 470

longicornis (Tokunaga) (1940); Tenthredo 3: 103
Tokunaga (1962), Pacific Insects 4(1): 186

nigeriae (Ingram and Macfie) (1924); Ann.Trop.Med.Parasitol. 18(3): 382

quasicornuta (Saunders) (1964); Can. J.Zool. 42: 467

townsvillensis (Taylor) (1914); Australian Zoologist 1(1): 169
Saunders (1964), Can.J.Zool. 42: 472

velox (Winn.) as pilosipennis(Kieffer) (1921); Arch. Inst. Pasteur
Afrique du Nord 1: 115

8. RE-EXAMINATION OF THE SYSTEMATIC POSITION OF THYRIDOMYIA SAUNDERS

Saunders (1964) did not include Thyridomyia species in the Lasiohelea complex because of the presence of an elongated second radial cell in the wing of the latter group, though the common group character of the single spermatheca in the female is shared between the two, and from all characters are much closer to each other than they are to other "subgenera" (except Dacnoforcipomyia) of the complex.

In the larva, both the subgenera Thyridomyia and Lasiohelea have the characteristically small hypognathous head, large eyes, presence of an ocular seta (not in all Thyridomyia species), four or more prominences on the vertex, general arrangement of hooks in a double ring on the anal pseudopod, scale-like cuticular armature and general distribution of the chaetae. The main differences, hitherto supposedly constant, are in the antennae and the abdominal *a* and *b* hairs. The reduced antennae of *Thyridomyia* larvae have been considered as constant characters but certainly the presence of reduced flagella of relative sizes on distinct tubercles in *palustris* Saunders (1925), *aspinosa* Saunders (1956) and 'sp. A' (Saunders, 1956) indicates that they are, to a certain extent, variable. Presumably the reduced thyridomyian type of antennae has lost some specific chemoreceptive function pertaining to life in mossy and woody situations or has acquired a different function.

The torch-like *a* and *b* setae of *Lasiohelea* larvae have also been considered to be constant characters of this "subgenus" but these again are present outside this "subgenus" in *Thyridomyia rugosa* and in *Thyridomyia aspinosa* on the first two thoracic segments and similar rudimentary ones on other segments. In *Thyridomyia nodosa* Saunders (1959) they are "rosette-like" (or practically "torch-like"). Careful examination and comparison of these setae in *Thyridomyia rugosa* and *Thyridomyia vertexcava* show that the long setae and their tubercles in the latter (Fig. 17 E) when shortened would be essentially torch-like, as in the former (Fig. 21B, Fig. 21F). The leaf-like processes on the tubercles of *Thyridomyia vertexcava* are still retained in rudimentary form, on the posterior side of the tubercles in *rugosa* (Fig. 21F).

Again, the ocular seta is not limited to *Lasiohelea* (and

Neoforcipomyia Tokunaga) alone but is also found in Thyridomyia aspinosa, Thyridomyia monilicornis Coquillett (1905) and Thyridomyia rugosa. The only real difference is the consistent absence of cauda in Thyridomyia species described so far and their presence in practically all Lasiohelea species, albeit modified. In the writer's opinion cauda are variable characters and may be present or absent in the same subgenus. For example, they are absent in Lasiohelea uncuspromissa Chan and present in most other species.

In the pupa, both Thyridomyia and Lasiohelea share many similar characters: (i) the short dorsal caudal projection which extends only to the middle of the first abdominal segment, (ii) the ventral male sexual processes (described by Saunders (1964) as 'dorsal' for Lasiohelea but corrected to 'ventral' in Chan and Saunders (1965)), (iii) the many dorsal tubercles on the thorax and abdomen, and (iv) the general plan of chaetotaxy. The only pupal character which appears to separate Thyridomyia from Lasiohelea is the shape of the prothoracic horn: broad distally with a narrow base in Thyridomyia and narrow with usually distinct 'heel' in Lasiohelea. In Thyridomyia rugosa the shape of the respiratory horn (Fig. 22 G) is more or less intermediate between the two, but actually closer to the latter: the base is narrow as in Thyridomyia and Lasiohelea but a posterior 'heel' as in Lasiohelea is also present. The distinction between the two subgenera is thus bridged by Thyridomyia rugosa.

The antennae of Thyridomyia and Lasiohelea females, however, seem fairly distinct; in females of the former only the distal four segments are distinctly longer than the basal ten, while in the latter the distal five are distinctly longer than the rest. In Thyridomyia nodosa and Thyridomyia rugosa the distal five segments are also fairly distinctly longer than the basal nine as in Lasiohelea females. As for immature stages, the female of Thyridomyia rugosa is intermediate in this character between the two subgenera. However, the similarities between characters of the females of both subgenera such as the single spermatheca, the wing costa ending beyond middle of the wing, the first radial cell slit-like or obliterated and the second radial cell distinctly longer than the first, are shared only by them (with the exception of Dacnoforcipomyia) and are distinctly different from the rest of the Forcipomyiinae.

The male genitalia have been considered to be reliable diagnostic characters in separating the two subgenera. Until recently, Lasiohelea males were reported to be consistent in their possession of a complicated aedeagus with chitinized recurved sclerites bearing hook-like outward-turning processes "highly differing from all other subgenera" (Tokunaga and Murachi, 1959). This supposedly reliable and constant character was shown by Saunders (1964) to be variable in that a few Lasiohelea species do not have outward-turning aedeagal hooks.

A close examination of the male genitalia shows that the basic natural components of the aedeagus are comparable in both Thyridomyia and Lasiohelea. Thyridomyia esakii Tokunaga (1940), Thyridomyia palustris Saunders (1925) and Thyridomyia nodosa Saunders (1959), for example, have aedeagi of essentially the same shape and structure as those of Lasiohelea quasicornuta Saunders (1964) and Lasiohelea intermedia Saunders (1964). Of singular conformity in all four species are the curved anterior lateral horns of the aedeagus and the two median longitudinal sclerites. The latter are of particular interest as they show tendencies of turning outwards in Lasiohelea longineura Saunders (1964), and Lasiohelea attenuata Saunders (1964), and Lasiohelea spinipenis Tokunaga (1959). The same general structure, though somewhat modified, is seen in Thyridomyia aspinosa Saunders (1956), and Thyridomyia hamata Tokunaga (1959) and in Thyridomyia rugosa, all three of which, on the basis of the structure of the aedeagus, are more closely related to each other, phylogenetically and taxonomically, than to the rest of the group.

It is therefore not surprising that expert taxonomists have on the basis of the male genitalia (immature stages were then not available) confused the two subgenera on at least two occasions: for example, Lasiohelea nana Macfie (1924) has been allocated to Thyridomyia nana by Saunders (1956) and Lasiohelea esakii Tokunaga (1940) to Thyridomyia esakii by Tokunaga himself (Tokunaga and Murachi, 1959).

It would appear then that the male genitalia of the typical Lasiohelea and the typical Thyridomyia differ only in the presence in the latter and absence in the former of the membranous window on segment 9 and in the structure of the claspettes - characters extremely variable according to Snodgrass (1957), but not without evolutionary significance.

Saunders' (1964) grouping of the subgenera Lasiohelea, Neoforcipomyia and Warmkea in the Lasiohelea complex, based on the arbitrary character of the elongated second radial cell is convenient but artificial since this classification does not show that these subgenera are more closely related to one another than to the rest of the Forcipomyia "subgenera". A thorough examination of characters in all stages of all the Forcipomyia "subgenera" show, beyond reasonable doubt, that the "subgenera" having closest affinity with Lasiohelea are Thyridomyia, Synthyridomyia and Dacnoforcipomyia.

In the light of these considerations and from comparisons with other "subgenera" of the Forcipomyiinae, as well as from the discovery of the immature stages of a sufficiently wide range of species, the writer is convinced that the distinction between Thyridomyia and Lasiohelea is not clear-cut and furthermore, the subgenera Synthyridomyia Saunders (1956), Thyridomyia Saunders (1925), and Dacnoforcipomyia Chan and Saunders (1965) may prove to be aberrant forms of Kieffer's (1921) genus Lasiohelea.

G. GENUS ATRICHOPOGON KIEFFER (1906)

1. SUBGENUS ATRICHOPOGON S. STR.

Type species levis (Coquillett) (1901) (syn. exilis Coq., 1910)

DIAGNOSIS

Larva.-

Head hypognathous, with antennae usually prominent, spur-like and rising from elongate socles; eyes prominent, dome-shaped, located anterodorsally on sides of head; vertex usually with longitudinal rows of rounded nodules; mouthparts well developed; pharyngeal skeleton bearing about six combs, pharyngeal angulus with bristles. Prothoracic pseudopod bilobed, each lobe with variable number of hooklets arranged in two rows, posterior row heavily sclerotized, dark and stout, and anterior row hyaline and slender. Posterior pseudopod bearing two transverse rows of varying number of hooklets, anterior row heavily sclerotized, dark and stout, posterior row hyaline and slender; anal papillae two. Body segments oval in cross section, with lateral processes often as long as segments; all body segments with short spines. Last abdominal segment with an unpaired sclerite on dorsum.

Pupa.-

Head separated from thorax by distinct furrow. Prothoracic horn short, boot-shaped, flattened or cylindrical depending on the aspect, and bearing in a curving row a varying number of spiracular papillae on posterior side. Thorax bearing six pairs of processes, decreasing in size posteriorly and may vary greatly in size; anteriormost two pairs nearest middle with spur-like seta. Posterior median point of mesothorax not overlapping first abdominal segment. Abdominal segments 2-7 dissimilarly bristled, first five segments usually with branched or setaceous projections. Male sexual processes ventral, short, protruding slightly beyond tip of abdomen. Larval exuviae retained in last three segments.

Adult Female.-

Body short, stout, slightly hairy; eyes bare or pubescent. Antennae with basal segments 3-10 globular, transverse and distal five segments elongate, usually much longer than basal segments. Mesonotum bare or with only short hairs. Legs slender with few or no hairs, end of foretibia usually with a setose anterior lobe; hind basitarsus always at least as long as the second segment. Wings broad, anal area rounded; microtrichia well developed, macrotrichia rather sparse, fine and suberect, often confined to wing tip or absent; costa reaching two-thirds of wing length; second radial cell long, usually two or three times as long as the first; cell R5 with conspicuous intercalary or folded fork; median fork with a stout stem, lower branch scarcely or not interrupted at base; anal vein straight; alula and squama bare; fringe on posterior body composed of a single row of alternating long and short, simple straight hairs. Abdomen sometimes with a median appendage on the sixth or seventh sternite; one or two spermathecae.

Adult Male.-

Antennae with weak verticels on segments 11-14, segment 11 not greatly lengthened. Other characters as in female with usual sexual differences. Genitalia with sternite 9 short, transverse, tergite 9 usually rounded, with anal processes; aedeagus usually simple, trilobed; claspettes absent or highly reduced, usually hook-shaped.

Species described in all stages.-

alveolatus Nielsen (1951); D. Kgl. Danske Videnskab. Selskab. Biol. Skrifter 6: 53

bifidus Ewen (1958); Can. J. Zool. 36: 694

carribeanus Ewen (1958); Can. J. Zool. 36: 683

corpulentus Ewen (1958); Can. J. Zool. 36: 681

cornutus Nielsen (1951); D. Kgl. Danske Videnskab. Selskab. Biol. Skrifter 6: 53

crinitus Ewen (1958); Can. J. Zool. 36: 717

dubius Nielsen (1951); D. Kgl. Danske Videnskab. Selskab. Biol. Skrifter 6: 52

flavus Ewen (1958); Can. J. Zool. 36: 697

fuscus (Meigen) (no data, coll. Goetghebuer)

hexastichus Nielsen (1951); D. Kgl. Danske Videnskab. Selskab.
Biol. Skrifter 6: 59

humicolus Ewen (1958); Can. J. Zool. 36: 679

incultus Ewen (1958); Can. J. Zool. 36: 699

inconspicuus Ewen (1958); Can. J. Zool. 36: 706

longicornis Ewen (1958); Can. J. Zool. 36: 700

levis (Coquillett) (1901); Proc. U.S. Nat. Mus. 23: 604
Ewen & Saunders(1958), Can. J. Zool. 36: 711

minutus (Meigen) (1830); Syst. Beschr. Eur. Zweifl. Ins. 6: 263
Ewen & Saunders (1958), Can. J. Zool. 36: 704

maculosus Ewen (1958); Can. J. Zool. 36: 689

obscurus Ewen (1958); Can. J. Zool. 36: 685

polydactylus Nielsen (1951); D. Kgl. Danske Videnskab. Selskab.
Biol. Skrifter 6: 61
Ewen & Saunders (1958), Can. J. Zool. 36: 715

remigatus Ewen (1958); Can. J. Zool. 36: 687

speculiger Nielsen (1951); D. Kgl. Danske Videnskab. Selskab.
Biol. Skrifter 6: 52

saundersi Ewen (1958); Can. J. Zool. 36: 691

tuberculatus Ewen (1958); Can. J. Zool. 36: 709

Other Species.-

Many other species are attributable to this subgenus on adult characters but these are not included here.

Ewen & Saunders (1958) have pointed out that, from characters of early stages, three or four groups in this subgenus may be separated and these may with further evidence, be recognized as new subgenera.

2. Subgenus Meloehelea Wirth (1956)

Type species meloesugans Kieffer (1922)

DIAGNOSIS

Same as for Atrichopogon except that adult females have long, upturned proboscis for attacking blister beetles of the family Meloidae. The following diagnosis is taken from Wirth (1956) and according to Wirth (loc. cit.) will set them apart from Atrichopogon (Atrichopogon) species:

"Eyes bare; proximal flagellar segments very short and disciform, the last five segments of the antennae together only 1.8 to 2.5 times as long as the preceding eight combined; palpal pit deep, near middle of third segment; mesonotum with a distinct light-colored area, or fenestra, just ahead of each end of the scutellum, extending forward as narrower, slightly impressed lines to the anterior margin of the mesonotum; scutellum with four long bristles; costa extending 0.65 to 0.70 way to tip of wing; hind basitarsus very nearly 2.5 times as long as the second segment; tarsal claws simple, not toothed or bifid at apices; empodium long, with many long tenent hairs with disc-like apices; two subequal, pyriform spermathecae".

Included Species.-

epicautae Wirth (1956); Proc. Entomol. Soc. Washington 58: 21

farri Wirth (1956); Proc. Entomol. Soc. Washington 58: 23

meloesugans Kieffer (1922); Arch. Inst. Pasteur Afrique du Nord 2: 495

oedemerarum Stora (1939); Notulae Ent. 19: 16

rostratus Winnertz (1852); Linn. Ent. 6: 1-80

3. THE SYSTEMATIC POSITION OF ATRICHOPOGON

Atrichopogon has been regarded as a distinct genus in the Forcipomyiinae since Edwards (1926) assigned it a generic status. This is emphasized by Johannsen (1943) who stated: "I consider that Atrichopogon merits a distinct position since it may readily be distinguished from the others on characters furnished by the larvae and pupae, and by the structure of the hypopygium of the male, as well as other structural features of the adult." In the light of Ewen and Saunders' (1958) recent paper, in which the immature stages and adults of 19 species of Atrichopogon were described, and from comparisons of these forms with other Forcipomyiinae, it would appear that Johannsen's statement requires correction.

In the classification erected so far the genus Atrichopogon has been separated from all other Forcipomyiinae groups principally by adult wing characters. Aside from these characters which are genuinely different from those of other Forcipomyiinae, there are decidedly no other characters in Atrichopogon by which the genus can be separated from the other members of the subfamily. Nielsen (1951) and Ewen and Saunders (1958) have pointed out that Atrichopogon should be defined on the basis of the larvae and/or pupae rather than on the adults, and the writer agrees that the early stages provide a better systematic basis for this genus.

On immature characters, the deciding difference between Atrichopogon and other Forcipomyiinae has been, for a long time, the flattened appearance of the larvae in this genus. This, as has been pointed out in the introduction is no longer valid since some Thyridomyia larvae also have the flattened appearance. *Atrichopogon* larvae have also been differentiated from other larvae by their lateral processes being in this genus at least as long as the body segments, but in other groups less than half the length of the segments. This differentiation is again no longer valid since larvae of *Schizoforcipomyia* have the *b* setae much longer than each body segment and the larvae of *Dacnoforcipomyia* and some *Thyridomyia* have the *a* (sometimes *b*) setae as long as each body segment. *Trichohelea* *nicopina* n. sp. also has the body setae longer than, or as long as, the segments.

Thomsen (1937) has separated *Atrichopogon* from other Forcipomyiinae on pupal characters, in addition to those of the larvae, pointing out that in this genus all pupae have on the first five abdominal segments projections, branched or setaceous, while in other Forcipomyiinae, all but the last abdominal segment bear either spines or stump-like projections. These characters again no longer hold true since *Atrichopogon* *polydactylus* has projections on all but the last abdominal segments and many *Atrichopogon* species do have small spines or projections on the fifth to seventh abdominal segments, and pupae of many other Forcipomyiinae do not bear projections at all on most abdominal segments. Ewen and Saunders' (1958) statement that there is no single character in the immature stages of *Atrichopogon* which can infallibly separate them from the early stages of other Forcipomyiinae is perhaps nearest to the truth. Hence, on the basis of the above evidence, no author has yet shown the true relationship between *Atrichopogon* and other Forcipomyiinae, nor has a true systematic position for the genus been reached.

Kieffer (1921) in his original definition of Lasiohelea, placed it as intermediate between Atrichopogon and Forcipomyia, ascribing to it the following: "Alar pilosity as in Ceratopogon (i.e. Forcipomyia) empodium as long as the claws, with short hairs; the rest as in Atrichopogon. Type Atrichopogon pilosipennis Kieff.".

Edwards (1922), like Kieffer, came nearest to the systematic position of Atrichopogon in the Forcipomyiinae in his discussion of Lasiohelea and would have most certainly reached the same conclusion as the writer had he had sufficient information on the immature stages. He (loc. cit.) pointed out the close morphological similarity between Atrichopogon and Lasiohelea, giving as an example the misidentification of Winnertz's Lasiohelea velox by Kieffer (1919) as Atrichopogon pilosepennis. Edwards (loc. cit.) further stated that Lasiohelea is intermediate between Atrichopogon and Forcipomyia, and that "it resembles the former genus in the structure of the antennae and in the venation, notably in the very long second radial cell, which extends well beyond the middle of the wing; the cell, however, is narrower than it is in Atrichopogon, the radius being almost in contact with the costa, while the first radial cell is obliterated by the fusion of r_1 and rs. On the other hand, the relationship to Forcipomyia is shown by the rather densely hairywings, though the hairs are less closely-lying than in Forcipomyia, and there are bare lines adjoining the veins, as in Atrichopogon. Among the larger hairs, which are spread over nearly the whole surface, can be distinguished small microtrichia, smaller than those of Atrichopogon, but more obvious than those of Forcipomyia."

Macfie (1932) also pointed out that "the genus *Lasiohelea* is intermediate between *Forcipomyia* and *Atrichopogon*, but it is not easy to find reliable characteristics by means of which it may be separated from the former." He regarded *Lasiohelea* as a sub-genus of *Forcipomyia*, and "as one stage beyond *Euforcipomyia* (i.e. *Proforcipomyia*) in the direction of *Atrichopogon*.

In the process of constructing keys for all stages of the genera of Forcipomyiinae the writer constantly encountered difficulty in separating the immature forms of *Atrichopogon* from those of the *Lasiohelea* group of Forcipomyiinae. This led to a comparative study of the two groups and all other groups of the Forcipomyiinae. As a result of the study the writer is now convinced that *Atrichopogon*, on the basis of Saunders' (1956) criteria for division of the 'genus' *Forcipomyia*, can be included as a subgenus of the latter, and that *Atrichopogon* is phylogenetically closest to the *Lasiohelea* group of Forcipomyiinae. This will be abundantly clear from the following considerations.

Structural similarities between *Atrichopogon* and the *Lasiohelea* group of Forcipomyiinae are numerous and are found in all stages of both genera. In the larva, the head capsule in both *Atrichopogon* and *Lasiohelea* are relatively small in size and are generally similar in shape. *Atrichopogon* larvae have typically a prominent antenna with elongated socle high on the head. This condition is found in the *Lasiohelea* subgenus *Synthyridomyia* and in the genus *Metaforcipomyia* which is here considered as very close to *Forcipomyia*. The ocular seta of *Atrichopogon*, erroneously interpreted as "seta 7" by Ewen and Saunders

(1958) and considered by them as "lacking in *Forcipomyia*" is always present except in *Atrichopogon crinitus*. This seta is also always present in *Lasiohelea* s. str., *Synthyridomyia* and in some *Thyridomyia* species. The only other genus in Forcipomyiinae sharing this character is *Neoforcipomyia* which, it must be pointed out, is closely related to both *Atrichopogon* and *Lasiohelea*. Another feature peculiar to these two genera is the irregular sculpture of the vertex, and of the lateral surfaces of the head, not found in other Forcipomyiinae except *Neoforcipomyia*. *Atrichopogon* larvae typically have five longitudinal rows of rounded nodules on the vertex. In *Thyridomyia* the number of "nodules" varies somewhat, usually being reduced through fusion or modification, to single "tubercles" or to complicated protuberances as in *Thyridomyia vertexcava*. In *Lasiohelea* s. str. these are reduced to four low prominences, in *Synthyridomyia* and *Dacnoforcipomyia* to two and in the subgenus represented by Lane's *Lasiohelea stylifer* Lutz, to a "reticulate pattern".

The body of *Atrichopogon* larvae is typically flattened in appearance due to the elongated lateral tubercles. This flattened appearance is also found, or at least approximated, in some *Thyridomyia* species (*monilicornis*, *vertexcava* n. sp. etc.) and also *Dacnoforcipomyia anabaenae*; the latter species are also characteristically adapted to the same type of habitat, namely moist surfaces covered with a thin layer of bryophytes. This flattened condition is absent in all other Forcipomyiinae. The anterior pseudopod of *Atrichopogon* larvae are divided, each ramus bearing two rows of hooklets, the anterior row of hooklets hyaline and slender, the posterior row of hooklets stout and heavily sclerotized. The divided pseudopod is also found in *Thyridomyia aspinosa* Saunders (1956) and again in all other *Lasiohelea* species except *Dacnoforcipomyia anabaenae*, the hooklets are composed of hyaline slender anterior ones and heavily sclerotized, stout, posterior ones. The divided pseudopod outside of these two genera is found only in *Forcipomyia* (*Forcipomyia* s. str., *Schizoforcipomyia*) but in these forms the hooklets are almost always monotypic and not arranged in rows but in a circle.

Another similarity between *Atrichopogon* and *Lasiohelea* found nowhere else in the Forcipomyiinae is the rare condition where a transverse band of sclerotized spines on the dorsum of each segment except the last, more or less connects the *a* hairs posteriorly as in *Thyridomyia monilicornis*, *palustris*, *vertexcava* n. sp. and *Atrichopogon humicolus* Ewen (1958).

In the pupa, the shape of the respiratory horn in *Atrichopogon* and *Lasiohelea* is not very different, especially between *Atrichopogon* and *Lasiohelea* s. str. where it is narrow and has a posterior "heel", often more pronounced in *Atrichopogon*. The median head sclerite in both genera typically and usually bears three tubercles, the anterior pair setigerous and the lateral head sclerites each usually and typically bears a setigerous tubercle. This condition is not seen in other Forcipomyiinae although the number of tubercles on the head sclerities may be the same. Another character found in both genera is the frequent occurrence on the dorsum of the thorax of six pairs of tubercles, of which the anteriormost towards the middle are setigerous. This condition again is found nowhere else in the

Forcipomyiinae. Again, another similarity is seen in the ventral position of the sexual processes in the male pupae. In both *Atrichopogon* and *Lasiohelea* the sexual processes are short, protruding just or slightly beyond the tip of the abdomen. This condition is also found in *Trichohelea* and *Neoforcipomyia* but the processes are much longer in the latter genus. A distinct difference, however, exists between pupae of *Atrichopogon* and *Lasiohelea*, notably the presence of branched or setaceous lateral processes usually on the first five abdominal segments in the former genus, and the absence of these processes in the latter genus. This difference is however not taxonomically important since in *Atrichopogon* the branched processes are structures adapted to life in moist situations and are modified setae homologous to a similar lateral group in *Lasiohelea*.

In the adult, similarities in characters between *Atrichopogon* and *Lasiohelea* are many. In both genera the maxillary palps are distinctly five-segmented. The basal antennal segments in *Atrichopogon* are globular or transverse and the distal five segments elongate, a condition found also in *Lasiohelea* s. str., *Dacnoforcipomyia* and the new subgenus (Lane's *Lasiohelea stylifer* Lutz). This condition is also found in *Trichohelea*, which is closely related to both *Atrichopogon* and *Lasiohelea*, despite the apparently distinctive immature stages that have evolved through adaptation to aquatic habitats in the leaf axils of plants.

In the wing of *Atrichopogon* the costa reaches to two-thirds the wing length and the second radial cell is elongated and always open. The costa in *Lasiohelea* s. str., *Dacnoforcipomyia*, new *Lasiohelea* subgenus (Lane's Lasiohelea stylifer Lutz) and some Thyridomyia species also reaches to about two-thirds of wing length and the second radial cell is elongated but usually practically closed. This condition of the wing is approximated by Califorcipomyia, Forcipomyia (Warmkea), Neoforcipomyia and some Trichohelea where the second radial cell is practically closed or somewhat open.

In the legs, the hind TR is larger than 2.0 and rarely slightly larger than 3.0 in Atrichopogon. In all subgenera of Lasiohelea the hind TR is also larger than 2.0 and usually less than 3.0. This large TR value is found only in two other genera of Forcipomyiinae, namely Trichohelea and Metaforcipomyia where only very few species have been described.

Most Atrichopogon females have only one spermatheca, a characteristic feature found in all Lasiohelea species. Other genera in the Forcipomyiinae with a single spermatheca are Neoforcipomyia, Pterobosca (some), Parapterobosca, Forcipomyia (Warmkea, some Schizoforcipomyia).

Superficially the genitalia of Atrichopogon would be considered distinctly different from those of Lasiohelea, but this apparent difference can be explained on a phylogenetical basis (see section on Phylogeny). The claspettes in Atrichopogon are either absent or usually simple, hook-shaped. The latter condition is approximated most closely by that in Thyridomyia species where the claspettes are triangular (or practically hook-shaped), which condition can be shown to be derived from the hook-shaped type (see Fig. 40).

The aedeagus in Atrichopogon is usually shield-shaped, trilobed, and with indications of two sclerotic thickenings running obliquely from the mesal point to the basal arch of the aedeagus. The aedeagus in *Lasiohelea* is also basically shield-shaped but usually highly modified, and often bipartite, with several sclerites, some with outward-turning tips as in many *Lasiohelea* s. str. In many species of *Thyridomyia* and *Lasiohelea* s. str. the aedeagus bears two sclerites from the mesal point to the basal arch, suggesting the later evolutionary result of similar thickenings in *Atrichopogon*.

The above similarities in all the stages between *Atrichopogon* and *Lasiohelea*, taken collectively show beyond reasonable doubt that these two genera are more closely related to each other than to other Forcipoymiinae. On the basis of these criteria *Atrichopogon* should be considered the closest to the *Lasiohelea* group in the Forcipomyiinae. An additional similarity further strengthens the contention. *Atrichopogon* species have parasitic habits like *Lasiohelea* species. Several *Atrichopogon* (*Meloehelea*) species have been observed to prey on other insects, e.g. *Atrichopogon meloesugans* on the beetle *Meloe majalis* Linnaeus in Algeria (Kieffer, 1922), and *Atrichopogon rostratus* (Winn. 1852) on a closely related beetle, *Meloe proscarabeus* Linnaeus in Denmark (Edwards, 1923), and *Atrichopogon oedemerarium* on *Meloe violacens* Marsham in Germany and Sweden (Wirth, 1956). From a physiological point of view, therefore, *Lasiohelea* and *Atrichopogon* are closely related. It may therefore be assumed that both *Atrichopogon* and *Lasiohelea* groups had a common ancestor in the distant past. This ancestor through adaptive radiation gave rise to forms which diverged from the basic phenotype mainly along two lines, principally in characters of the wing, presumably associated with feeding habits of the adults, and in a few immature characters, e.g. branched processes of pupal abdominal segments and flattened larval appearance, presumably associated with life in semi-aquatic habitats like water-soaked bryophyles (mosses, liverworts and algae).

H. GENUS *NEOFORCIPOMYIA* TOKUNAGA (1959)

Type species *Forcipomyia pectinunguis* de Meijere (1923)

DIAGNOSIS

Larva.-

Length of full grown fourth instar about 3 mm. Color yellow when cleaned of coating of foreign particles. Body rather stout, with sides of segments projecting when seen dorsally. Head comparatively small, strongly hypognathous, depressed under prominent prothorax; two or four low prominences on vertex; eyes prominent, dome-shaped, halfway down front of head, with ocular setae; antennae below eyes, small, slender, on low socle; *q*, *s* and *t* hairs simple, slender, on low tubercles. Prothoracic dorsum with two pairs of large hook-tipped setae on long slender tubercles. *a* hairs lacking or when present, small. Abdominal segments all except last with lateral tubercles bearing complex rosette setae; penultimate segment with one pair dorsal setigerous tubercles similar to those on prothorax, or shorter and broader. Prothoracic pseudopod undivided, relatively short, with two groups of hooklets, an anterior group of three hyaline, slender ones and a posterior group of five strongly sclerotized, stouter ones, on each side of the mid-line. Posterior pseudopod with nine pairs black hooklets in almost complete double ring around anus. Cauda absent but last segment may bear paired cauda-like structures, setose or smooth. Cuticular armature hair-like, short or long on ventral surface.

Pupa.-

1.5-2.3 mm. Inner color yellow as in larva, exuviae faintly pigmented on thorax. Median head sclerite with well developed tubercles. Thorax and abdomen with small to rudimentary tubercles, abdomen sometimes with diagonal cuticular markings. Median posterior point of mesothorax just overlapping anterior border of first abdominal segment. Prothoracic respiratory horn variable in shape and arrangement of spiracular papillae. Terminal processes short in both sexes, sharply out-turned in male, less so in female. Male sexual processes ventral. Larval ex uviae retained in last three segments.

Adult Female.-

Basal flagellar segments of antenna subspherical, distinctly shorter than distal five segments and never flask-shaped. Maxillary palp completely segmented. Hind TR greater than 2.4; empodia and claws normal. Wings unadorned, rather densely haired with slender macrotrichia; costa reaching beyond middle of wing, second radial cell narrow, long, and at least as long as first, first radial cell obliterated and slit-like. Two spermathecae.

Adult Male.-

AR 1.0 or greater. Hind TR 2.3-3.2; empodia of legs lacking or vestigial. Genitalia with claspettes arch-like, as in Proforcipomyia but massive and usually with spoon-shaped caudal lobes; aedeagus somewhat shield-shaped; sternite 9 much shorter than wide and without deep caudal emargination.

Neoforcipomyia saundersi CHAN NEW SPECIES

DIAGNOSIS

This new species is named in honour of Dr. L.G. Saunders in recognition of his great contribution to the taxonomy of the Forcipomyiinae.

Egg.-

Elongate, ovoid, well rounded anteriorly (micropylar end) and less so posteriorly (Fig. 31A). Length 277.59 ± 3.58 μ, greatest width and depth 91.03 ± 2.12 μ. Color black; exochorion smooth, without ornamentation. On hatching it splits along the dorsal surface from anterior end to about 5/8 of its length. Eggs laid singly or in masses of irregular shapes and sizes.

Larva.-

Length of full-grown fourth instar larva (Fig. 31B) 2.69 ± 0.25 mm. Color in life lemon yellow to light brown with internal contents brown to dark grey. Head black; chaetotaxy as in *Forcipomyia* (*Neoforcipomyia*) *crinita* Saunders (Saunders, 1964) but with a single pair of conspicuous prominences on vertex. Eyes, antennae and setae as in Fig. 31C. HR 1.46 ± 0.05; AR 7.43 ± 0.97· qt/ts/sq 1.35 ± 0.13: 1.60 ± 0.15: 1; tt/ant 0.41 ± 0.08; qq/eyes 0.52 ± 0.01; qq/ss 0.41 ± 0.0.

Prothorax with four large hook-tipped setae, seta *a* with filament and tubercle in proportion of 1.10 ± 0.17: 1 and seta *b* with filament and tubercle in proportion of 1.30 ± 0.12: 1; prothoracic pseudopod (Fig. 31D) with length, width and depth in proportion of 1.47 ± 0.24: 1.12 ± 0.23: 1. Unlike crinita the metathorax possesses *a* hairs.

Abdominal chaetotaxy as in crinita but with *a* hairs on segments

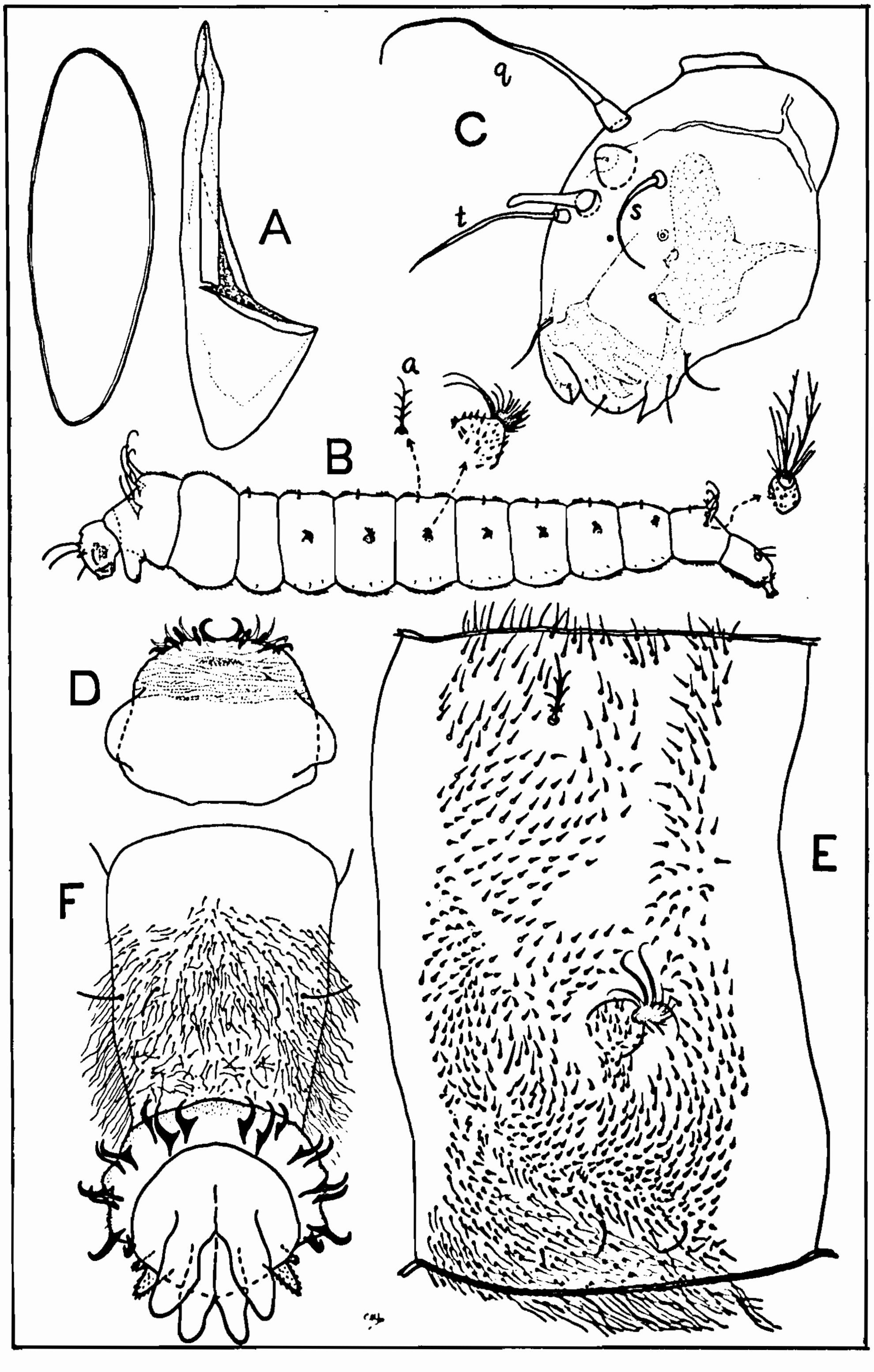
Fig. 31. <u>Neoforcipomyia</u> <u>saundersi</u> n. sp.

A, Egg

B-F, Fourth-instar larva:

- B, Larva, lateral view
- C, Head
- D, Prothoracic pseudopod
- E, Third abdominal segment
- F, Last abdominal segment, ventral view

Fig. 31



1-8 and with fine, smaller hairs on ventral surface (Fig. 31B, 31E). Last abdominal segment bearing dorsal plate with two short, setulose spines as in crinita (Fig. 31B) but with paired unequally bilobed structures on dorsal extremity, and four anal papillae (Fig. 31F).

Cuticular armature hair-like (Fig. 31B, 31E), with definite pattern throughout body; those on dorsal surface directed anteriorly in prothorax and mesothorax and posteriorly in last two segments, the rest of the segments each bearing two groups (anterior and posterior) the anterior group directed posteriorly and the posterior group directed anteriorly or vertically. (This arrangement of cuticular armature on the dorsal surface is undoubtedly associated with holding of foreign particles for cryptic purposes). Cuticular armature on ventral surface hair-like, hairs long and directed posteriorly.

Pupa.-

Length 1.94 ± 0.09 mm. in female and 2.13 ± 0.09 mm. in male. Color as in larva but dark near emergence of adult.

Median head sclerite with three well-developed tubercles, shagreened anterior pair spiniferous; lateral sclerites devoid of tubercles (Fig. 32A). Cephalothorax 1.73 ± 0.02 times longer than its greatest breadth in female and 1.77 ± 0.06 in male. Ratio of length of head to thorax 0.49 ± 0.03 in ventral aspect and 0.19 ± 0.03 in dorsal aspect in female and respectively 0.51 ± 0.04 and 0.27 ± 0.06 in male.

Thorax bearing four pairs of rudimentary tubercles, one pair of transverse, elliptical markings suggesting tubercles, and two anterior median ridges (Fig. 32A). Prothoracic horn as in crinita but with 8-12 spiracular papillae, 2.34 ± 0.29 times as long as its greatest width in female and 2.35 ± 0.30 in male; tracheal length in horn to horn length 0.59 ± 0.08: 1 in female and 0.65 ± 0.05: 1 in male.

Abdominal segments 1-8 with one median tubercle flanked by two diagonal cuticular markings as in crinita but segments 3-7 each bears, in addition, a pair of minute tubercles with setae (Fig. 32A) lateral to the diagonal markings; segment 7 bears still another pair of small conical tubercles, lateral to the tubercles; lateral tubercles on segments 3-7 small, conspicuous and bear minute setae. Cuticle of entire abdomen very finely shagreened. In female length, width, depth of third segment in proportion of 1: 2.12 ± 0.10: 1.88 ± 0.14 and that of last segment 1.12 ± 0.12: 1: 1.05 ± 0.08. In male similar ratios for third abdominal segment 1: 2.10 ± 0.15: 1.89 ± 0.13 and for sexual processes 3.51 ± 0.29: 1.01 ± 0.12: 1.

Adult Female.-

Body length 1.56 ± 0.10 mm. Wings 0.91 ± 0.10 mm. by 0.43 ± 0.02 mm.

Head dark, with antennae and mouthparts dark brown. Maxillary palp stout, with third segment bearing large shallow sensory pit (Fig. 32C); PR 1.45 ± 0.10. Antenna dark brown, AR 2.20 ± 0.16 (Fig. 32B).

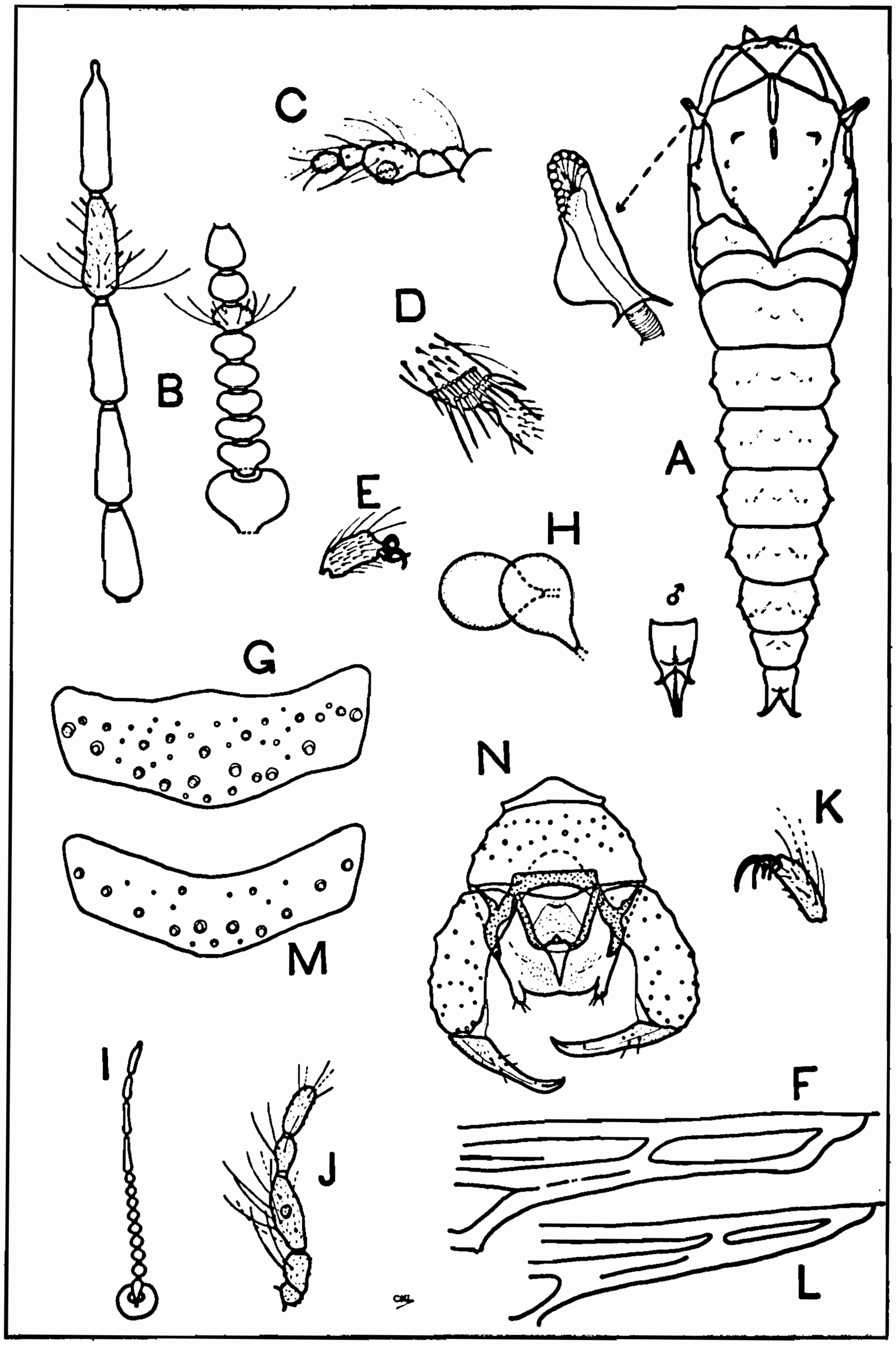
Thorax dark brown, scutellum with bristle arrangement as shown (Fig. 32G). Legs brown; fore TR 2.81 ± 0.08; mid TR 2.69 ± 0.09; hind TR 2.88 ± 0.08; claws (Fig. 32E) normal; empodium large; apical tibial comb with 7 or 8 bristles (Fig. 32D).

Wings pale brown with veins dark brown; CR 0.56 ± 0.01. Venation: vLR 1.19 ± 0.07: 1: 2.18 ± 0.17; rs/r_1 2.04 ± 0.07;

Fig. 32. Neoforcipomyia saundersi n. sp.

A, Pupa: dorsal view
B-H, Adult female:
  B, Antenna
  C, Maxillary palp
  D, Hind tibial comb
  E, Last hind tarsal segment
  F, Stigmal area of wing
  G, Scutellum
  H, Spermathecae
I-N, Adult male:
  I, Antenna
  J, Maxillary palp
  K, Last hind tarsal segment
  L, Stigmal area of wing
  M, Scutellum
  N, Genitalia

Fig. 32



first radial cell slit-like, second radial cell somewhat narrow, slightly longer than first (1.26 ± 0.15: 1); fmcu under about middle of second radial cell. m_{3+4}/cu_1 1.77 ± 0.06. Haltere light brown with knob white.

Abdomen including cerci entirely brown; spermathecae (Fig. 32H) two, almost spherical, about equal, with short duct, measuring 261 ± 13.4 μ by 234 ± 14.5 μ and 278 ± 12.8 μ by 242 ± 14.9 μ, and their ducts respectively 59.3 ± 10.3 μ and 58.5 ± 4.8 μ.

Adult Male.-

Body length 1.81 ± 0.09 mm. Wings 1.05 ± 0.01 mm. by 0.35 ± 0.02 mm.

Head dark with antennae and mouthparts brown. Maxillary palp (Fig. 32J) rather slender, with segment 3 bearing shallow, small sensory pore just beyond middle; PR 2.25 ± 0.29. Antenna (Fig. 32I) entirely brown, AR 1.15 ± 0.04.

Thorax dark brown; scutellum (Fig. 32M) with variable number of bristles (8-10 large). Legs brown, tarsal segments slightly paler brown; fore TR 2.42 ± 0.09, mid TR 2.33 ± 0.13; hind TR 2.68 ± 0.11; claws (Fig. 32K) slender, empodia lacking; apical tibial comb with seven or eight bristles.

Wings pale brown, with veins brown; CR 0.51 ± 0.01. Venation: vLR 1.16 ± 0.03: 1: 1.90 ± 0.15. rs/r_1 1.88 ± 0.12: 1; first radial cell slit-like, second radial cell narrow, about as long as first (1.00 ± 0.13: 1) (Fig. 32L); fmcu under about the end of costa; m_{3+4}/cu_1 2.33 ± 0.09. Haltere brown with knob white.

Abdomen brown. Genitalia (Fig. 32N): sternite 9 about half as long as wide (0.50 ± 0.03: 1); tergite 9 more than half as long as wide (0.59 ± 0.05: 1). Parameres with basimeres slightly curved, about $2\frac{1}{2}$ times as long as wide (2.61 ± 0.15: 1) and telomeres curved and pointed at tip and about seven times longer than its greatest width (7.35 ± 0.46: 1); aedeagus funnel-shaped, caudo-lateral shoulders and their distal transverse connection heavily sclerotized, mesal point diamond-shaped, pointed apically, length and width of aedeagus in proportion of 1.02 ± 0.10: 1; claspettes a massive square-topped arch with basal arms extended posteriorly into spoon-shaped lobes, the two basal arms and basal union of claspettes subequal in length, right arm to basal union to left arm in proportion of 1.09 ± 0.10: 1: 1.07 ± 0.15.

Holotype (fourth instar larva).-

Collected from May to September, 1964, on decaying wood with a thin growth of algae and young moss, in Morgan Arboretum, Macdonald College, Quebec, Canada. Deposited in Lyman Entomological Museum, Macdonald College.

Paratypes.-

Many males, females,with associated pupal exuviae, and larvae collected from same habitat. In Lyman Entomological Museum, Dr. L.G. Saunders' and personal collections.

The larva of this species is very close to that of crinita Saunders (1964) in the four large hook-tipped prothoracic setae, similar setae on the penultimate segment, in the lateral abdominal setal complex and in the arrangement of hooks on the prothoracic pseudopod; it differs however in the possession of a abdominal setae, in the finer hair-like ventral cuticular armature, in the single prominence on the vertex of the larval head and in the possession of a paired unequally lobed, finely setulosed structure on the dorsal extremity of the last segment. The pupa of this species also resembles that of *crinita* in the shape of the respiratory horn and in the cuticular markings on the abdominal segments; it differs however in the less sharply outward-turning terminal processes and in the possession of a pair of minute setae lateral to the cuticular markings on the dorsum of the abdominal segments. The male genitalia are also very close to those of *crinita*, especially in the aedeagus but differ in having claspettes with spoon-shaped caudal lobes.

Neoforcipomyia eques (Johannsen)

Ceratopogon eques Johannsen,(1908;)Bull New York State Mus. 124,266

Pseudoculicoides eques Smith,(1922); Cornell Univ. Agr.Exp. Sta.Mem. 58: 1341

Forcipomyia (*Euforcipomyia*)*eques* Edwards (1924); Notulae Ent. 4: 97; Forsius (1924) iden. 4: 97

Forcipomyia (*Apelma*) *eques* Edwards (1932); Ent. Mo. Mag. 68: 114

Forcipomyia chrysopae Mayer (1934); Arb. Morph. Tax. Ent. Berlin-Dahlem 1: 259

Lasiohelea chrysopivora Tokunaga (1939); Volumen Jubilare pro Prof. Sadao Yoshida 2: 371

Forcipomyia eques Tjeder (1936); Notulae Ent. 16: 85; Tjeder, (1944): Bergens Mus. Arbok 1944 Nat. Rek. 1: 10; Wirth (1956), Ann. Ent. Soc. Amer. 49: 358-9

Forcipomyia (*Neoforcipomyia*) *eques* Saunders (1964); Can. J. Zool. 42: 478

Eggs, fourth instar larvae and pupae are described for the first time while adults are redescribed. The following redescriptions of males and females, based on measurements of ten specimens of each sex, with illustrations of the important characters, is an attempt to redefine more accurately males and females of this species, which, it must be pointed out, has been frequently misidentified despite Johannsen's detailed original description (vide Wirth, 1956).

Egg.-

Elongate, ovoid, well-rounded anteriorly (micropylar end) and less so posteriorly. Length 278.22 ± 2.96 μ, greatest width and depth 91.18 ± 1.97 μ. Color black; exochorion smooth, without ornamentation. On hatching it splits along dorsal surface from anterior end to about 5/8 its length. Eggs laid singly or in masses of irregular shapes and sizes.

Larva.-

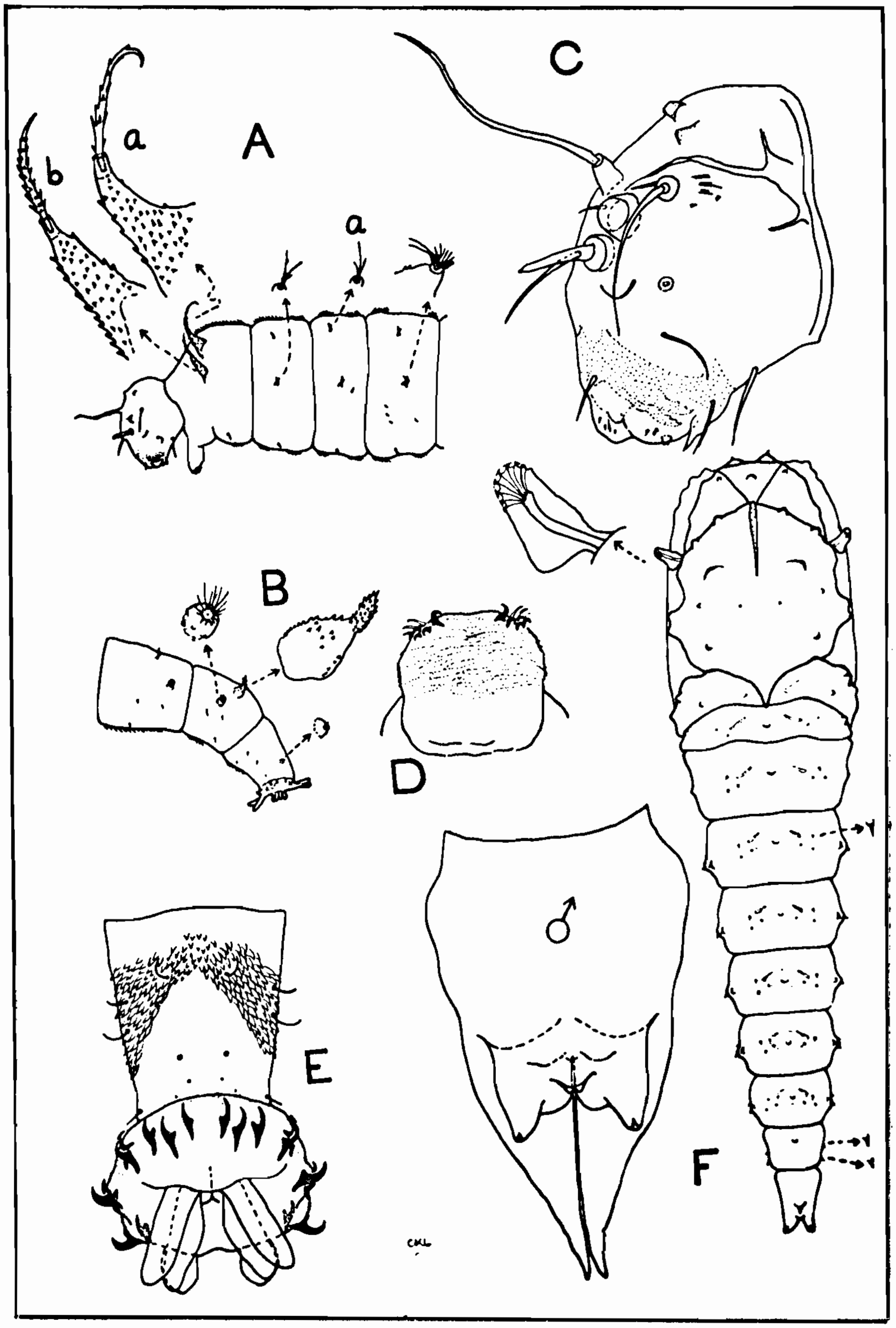
Length of full-grown fourth instar (Fig. 33A, Fig. 33B) 2.60 ± 0.21 mm. Color in life lemon yellow to orange with internal contents brown to grey. Head dark, with s hairs bearing secondary seta on dorsal surface of large basal tubercle. Two pairs of prominences on vertex low but distinct; eyes, antennae and setae as in Fig. 33C. HR 1.40 ± 0.03; AR 7.04 ± 0.39; qt/ts/sq in proportion of 1.57 ± 0.16: 1.43 ± 0.15: 1; tt/ant 0.46 ± 0.01· qq/eyes 0.53 ± 0.01; qq/ss 0.47 ± 0.01.

Prothorax with four large hook-tipped setae, seta a with filament and tubercle in proportion of 1.23 ± 0.08 and seta b with filament and tubercle in proportion of 1.20 ± 0.10; prothoracic

Fig. 33. <u>Neoforcipomyia</u> <u>eques</u> (Johannsen)

A-E, Fourth-instar larva:
  A, Anterior region
  B, Last three segments
  C, Head
  D, Prothoracic pseudopod
  E, Anal pseudopod
F, Pupa: dorsal view

Fig. 33



pseudopod (Fig. 33D) with length, breadth and depth in proportion of 1.29 ± 0.09: 1.88 ± 0.04: 1 and bearing three anterior pairs of hyaline hooklets and five posterior pairs of dark hooklets.

Abdominal chaetotaxy as shown (Fig. 33A, Fig. 33B); a seta of penultimate segment torch-like borne on a conical tubercle; last abdominal segment bearing minute, dorsal plate (Fig. 33B) with a rosette of very minute setae, and with a pair of single-lobed structures on dorsal extremity (Fig. 33E).

Cuticular armature scale-like (Fig. 33A, Fig. 33B, Fig. 33E) with the same arrangement on dorsal surface as in saundersi, that on ventral surface arranged in groups, all of which (except the mesothoracic) are directed backwards, presumably for grip during locomotion; mesothoracic ventral anterior group as in other segments but posterior group directed posteriorly in anterior portion and anteriorly in posterior portion (Fig. 33A).

Pupa.-

Length 1.76 ± 0.11 mm. in female and 1.94 ± 0.09 mm. in male. Color as in larva but dark near emergence of adult.

Median head sclerite with three well-developed tubercles, shagreened; median tubercle (Fig. 33F) without seta; lateral sclerites each with a minute, rudimentary tubercle near anterior end on inner edge (Fig. 33F). Cephalothorax 1.80 ± 0.05 times longer than its greatest width in female and 1.85 ± 0.07 in male. Length of head to thorax in proportion of 0.44 ± 0.04: 1 (ventral aspect) and 0.20 ± 0.03: 1 (dorsal aspect) in female and respectively 0.50 ± 0.02: 1 and 0.25 ± 0.03: 1 in male.

Thorax bearing four pairs of rudimentary tubercles and an anterior median ridge (Fig. 33F). Prothoracic respiratory horn short, greatest width immediately beyond the short narrow base (Fig. 33F) and bearing six or seven or eight spiracular papillae. Respiratory horn 1.66 ± 0.14 times longer than its greatest width in female and 1.58 ± 0.19 in male. Horn tracheal length to horn length o.72 ± 0.04: 1 in female and 0.73 ± 0.06: 1 in male.

Abdominal segments 1-7 with one median dorsal tubercle flanked by two diagonal cuticular markings as in crinita and saundersi and three pairs of dorso-lateral minute tubercles lateral and posterior to the markings, the three on each side forming roughly a triangle, the foremost bearing a minute seta; segment 8 bearing a dorsal tubercle, without diagonal markings; segments 1-8 each with a group of 2 or 3 lateral minute tubercles bearing very minute setae (Fig. 33F). In female length: width: depth of third segment in proportion of 1: 2.32 ± 0.30: 2.08 ± 0.38 and in male 1: 2.27 ± 0.43: 1.92 ± 0.27. Similar ratios for last segment of female are 1.21 ± 0.13: 1: 0.98 ± 0.13 and for sexual processes of male 3.04 ± 0.25: 1.17 ± 0.13: 1.

Adult Female.-

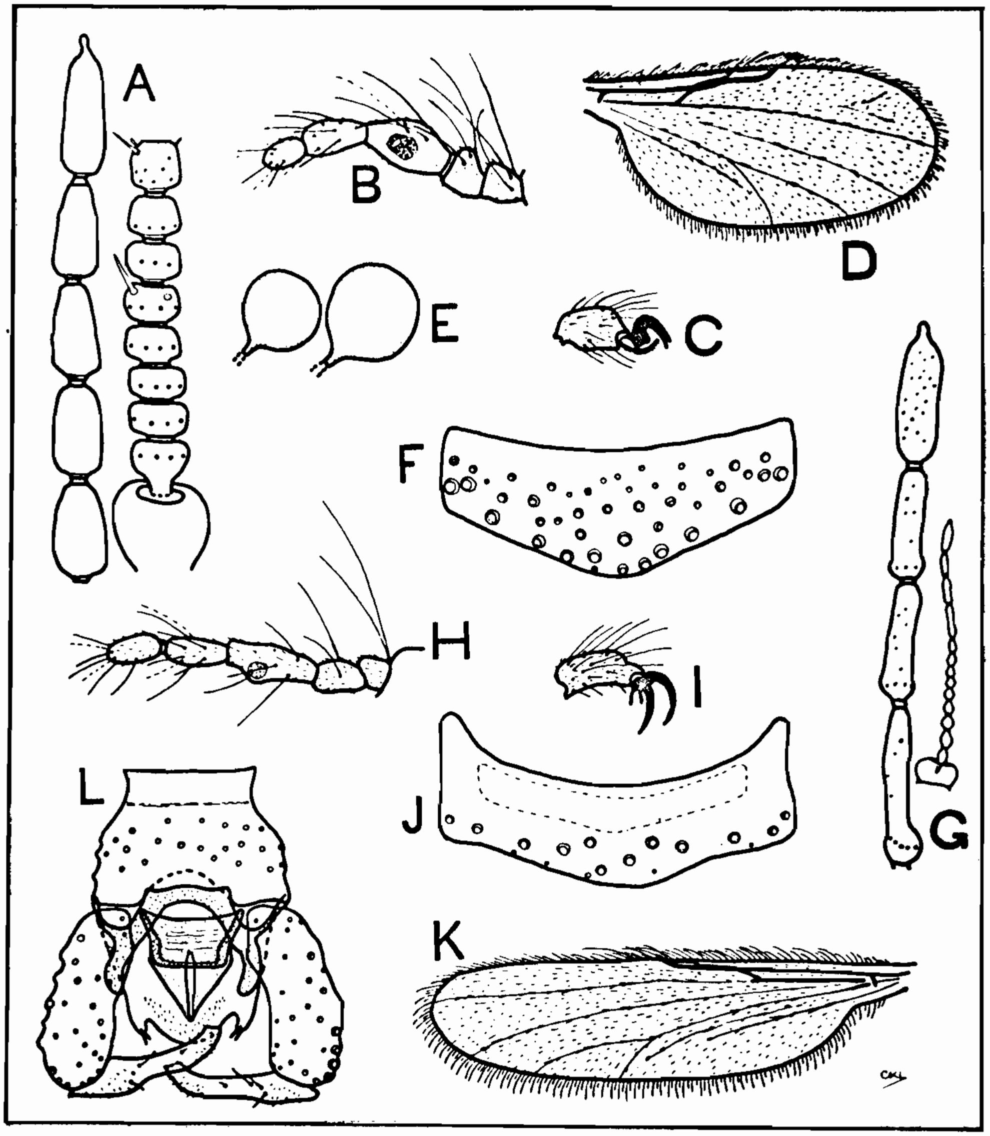
Body length 1.41 ± 0.14 mm. Wing (Fig. 34D) 0.88 ± 0.07 mm. by 0.41 ± 0.01 mm.

Head including antennae and mouthparts dark brown; eyes bare, contiguous above, occipital setae curved forward. Maxillary palp (Fig. 34B) with third segment bearing a small, deep pit; PR 1.73 ± 0.11. Antenna (Fig. 34A) entirely dark brown, AR 1.50 ± 0.10.

Fig. 34. Neoforcipomyia eques (Johannsen)

A-F, Adult female:
  A, Antenna
  B, Maxillary palp
  C, Last tarsal segment of hind leg
  D, Wing
  E, Spermathecae
  F, Scutellum
G-L, Adult male:
  G, Antenna
  H, Maxillary palp
  I, Last hind tarsal segment
  J, Scutellum
  K, Wing
  L, Genitalia

Fig. 34



Thorax brown; scutellum yellowish-brown, with bristle arrangement as shown (Fig. 34F); legs light brown; fore TR 2.41 ± 0.09, mid TR 2.36 ± 0.08, hind TR 2.53 ± 0.13; claws with stout basal swelling (Fig. 34C); empodium normal and large; tibia with seven or eight tibial spines.

Wing brown, covered all over with dark hairs, veins brown; CR 0.53 ± 0.02; vLR 1.26 ± 0.02: 1: 2.31 ± 0.06; rs/r_1 2.16 ± 0.13; first radial cell slit-like, and slightly shorter than second radial cell (1: 1.28 ± 0.30); m_{3+4}/cu_1 1.78 ± 0.02; fmcu under end of first radial cell. Halteres pale brown with white knobs.

Abdomen including cerci entirely brown. Spermathecae (Fig. 34E) two, almost spherical, subequal, with moderately long, thin, sclerotized ducts; and measuring 255 ± 15.8 μ by 240 ± 14.8 μ and 222 ± 11.8 μ by 207 ± 11.8 μ and their ducts respectively 46.5 ± 4.7 μ and 40.5 ± 3.0 μ.

Adult Male.-

Body length 1.67 ± 0.06 mm. Wings (Fig. 34K) 1.00 ± 0.02 mm. by 0.34 ± 0.02 mm.

Head mainly dark brown with antennae and mouthparts lighter brown. Maxillary palp rather slender, with segment 3 not swollen and bearing shallow, moderately large sensory pore (Fig. 34H); PR 2.33 ± 0.12. Antenna entirely brown, AR 0.98 ± 0.05 (Fig. 34G).

Thorax dark brown; scutellum (Fig. 35J) with bristle arrangement as shown. Legs pale brown; fore TR 2.19 ± 0.15, mid TR 1.96 ± 0.10, hind TR 2.30 ± 0.15; claws slender (Fig. 34I), empodia lacking; apical tibial comb of hind leg with seven or eight bristles.

Wing (Fig. 34K) pale brown, with veins brown and with narrow bare areas along veins; CR 0.48 ± 0.o2. Venation: vLR 1.16 ± 0.02: 1: 2.06 ± 0.19; rs/r_1 2.08 ± 0.59; first radial cell slit-like, second radial cell narrow and longer than first (1.22 ± 0.18: 1); fmcu under about end of costa; m_{3+4}/cu_1 2.22 ± 0.24. Haltere brown, with knob white.

Abdomen brown. Genitalia (Fig. 34L): sternite 9 more than half as long as wide (0.61 ± 0.01: 1), tergite 9 wider than long (1: 0.67 ± 0.02) and with convex caudal margin. Parameres with basimeres slightly curved, more than $2\frac{3}{4}$ times as long as wide (2.88 ± 0.20: 1) and with telomeres curved at apical one-third, outer margin indented at basal third, flattened at tip, about $5\frac{1}{2}$ times as long as greatest width (5.43 ± 0.40: 1); aedeagus funnel-shaped, anterior half sclerotized with marginal and transverse thickening, posterior half membranous with elongate median rod (mesal point), aedeagal length to width in proportion of 1.11 ± 0.16: 1; claspettes a massive arch with basal arms extended caudally into spoon-shaped lobes, the two basal arms and basal union of claspettes subequal in length (1.27 ± 0.12: 1: 1.27 ± 0.12).

Species described in all stages.-

crinita (Saunders) (1964); Can. J. Zool. 42: 474

trinidadensis (Saunders) (1964); Can. J. Zool. 42: 476

Other species.-

The following list is assembled by Saunders (1964):

"A. Identified by male genitalia

pectinunguis (de Meijere) (1923); Tijdschr. Entomol. 66: 138;
Wirth (1956); Ann. Entomol. Soc.Am. 49: 360
Tokunaga and Murachi (1959); Insects of Micronesia 12(3): 200

eques (Johannsen) (1908); Bull. N.Y. State Mus. 124: 266
Wirth (1956); Ann. Entomol. Soc. Am. 49: 358

basiflava (Tokunaga) (1959); Insects of Micronesia 12(3): 202

mcateei (Wirth) (1956); Ann. Entomol. Soc. Am. 49: 359

Four Australian and Tasmanian species in U.S.N.M.

B. Identified by females ectoparasitic on insects (data assembled by Wirth (1956)

okadai (Tokunaga) (1939); Vol. Jubil. Yoshida 2: 370

papillionivora (Edwards) (1923); Ann. Trop. Med. Parasitol. 17: 23

aeronautica (Macfie) (1925); Stylops 4: 265

baueri (Wirth) (1956); Ann. Entomol. Soc. Am. 49(4): 361

mexicana (Wirth) (1956); Ann. Entomol. Soc. Am. 49: 361

tipulivora (Macfie) (1936); Proc. Roy. Entomol. Soc. London (B) 5:230

insignicornis (Macfie) (1947); Proc. Roy. Entomol. Soc. London (B) 16: 29

equitans (Edwards) (1933); J. Federated Malay States Museums 17: 251

intrepida (Macfie) (1936); Proc. Roy. Entomol. Soc. London (B) 5: 228

pennambula (Macfie) (1932); Tidschr. Entomol. 75: 279

samoensis (Edwards) (1928); Insects of Samoa 2(4): 23-102

opilionivora (Lane) (1947); Arq. Fac. Hig. Saude Publ. Univ. S.Paolo 1: 159

I. GENUS TRICHOHELEA GOETGHEBUER (1920)

Type species auronitens Kieffer (1919)

DIAGNOSIS

The following diagnosis of the immature stages is taken from Saunders (1956):

"Larva.-

Head flattened, roughly rectangular with ratio of length to width variable between species, prognathous; antennae reduced to circular "windows" on front corners of head, containing minute sensoria. Body elongate, vermiform, cylindrical, with many fine lateral chaetae, sclerotized, crossbar on posterior margin of penultimate segment; cuticle devoid of armature. Prothoracic pseudopod conical, bearing many curved, hair-like hooklets beyond a row of short, stout hooks. Anal pseudopod a transverse row of ten black thorn-like hooks and a second row of eight slender, hyaline hooklets, the outermost usually stouter and serrate on inner surface. Body ending in a dorsal, median, bluntly conical point not turning up but still to be regarded as a cauda. Anal blood gills two pairs, bifircate or trifurcate, fine, pointed.

Pupa.-

Elongate, agile, never retaining larval exuviae. Chaetae few to none on thorax, numerous spines and short chaetae on sides of abdomen. Terminal rami wide-spaced, short, with small chaeta on outer surface; genital processes of male ventral short. Prothoracic horn small, narrow base, with U-shaped row of spiracular papillae at tip."

Adult Female.-

Basal flagellar segments of antenna compressed, sometimes reduced to five segments, discoidal to spherical, distinctly shorter than distal five segments; segments 7 to 9 sometimes slightly longer than wide, short-oval. Maxillary palp with segments 4 and 5 completely or incompletely segmented. Legs without scales; hind TR usually 2.0 to 3.2, rarely less than 2.0; empodia well developed, claws normal. Wings unadorned, thinly scaled, bare areas along veins indistinct; costa reaching at about or beyond middle of wing; first radial cell very slightly opened, slit-like or closed; second radial cell opened, as long as or slightly longer than first cell. Two spermathecae.

Adult Male.-

Empodia usually absent or vestigial, but fully developed in a few species. Male genitalia with sternite 9 broad and short; claspettes H-shaped, with crossbar joining bases of basal arms and with spoon-shaped caudal lobes extending posteriorly from bases of basal arms; aedeagus shield-shaped, broad and variable, rarely with caudal processes.

Trichohelea nicopina CHAN NEW SPECIES

Larva.-

Length of full grown fourth instar larva (Fig. 35A) 3.45 (3.15-3.75) mm. Body cylindrical, only head flattened dorso-ventrally.

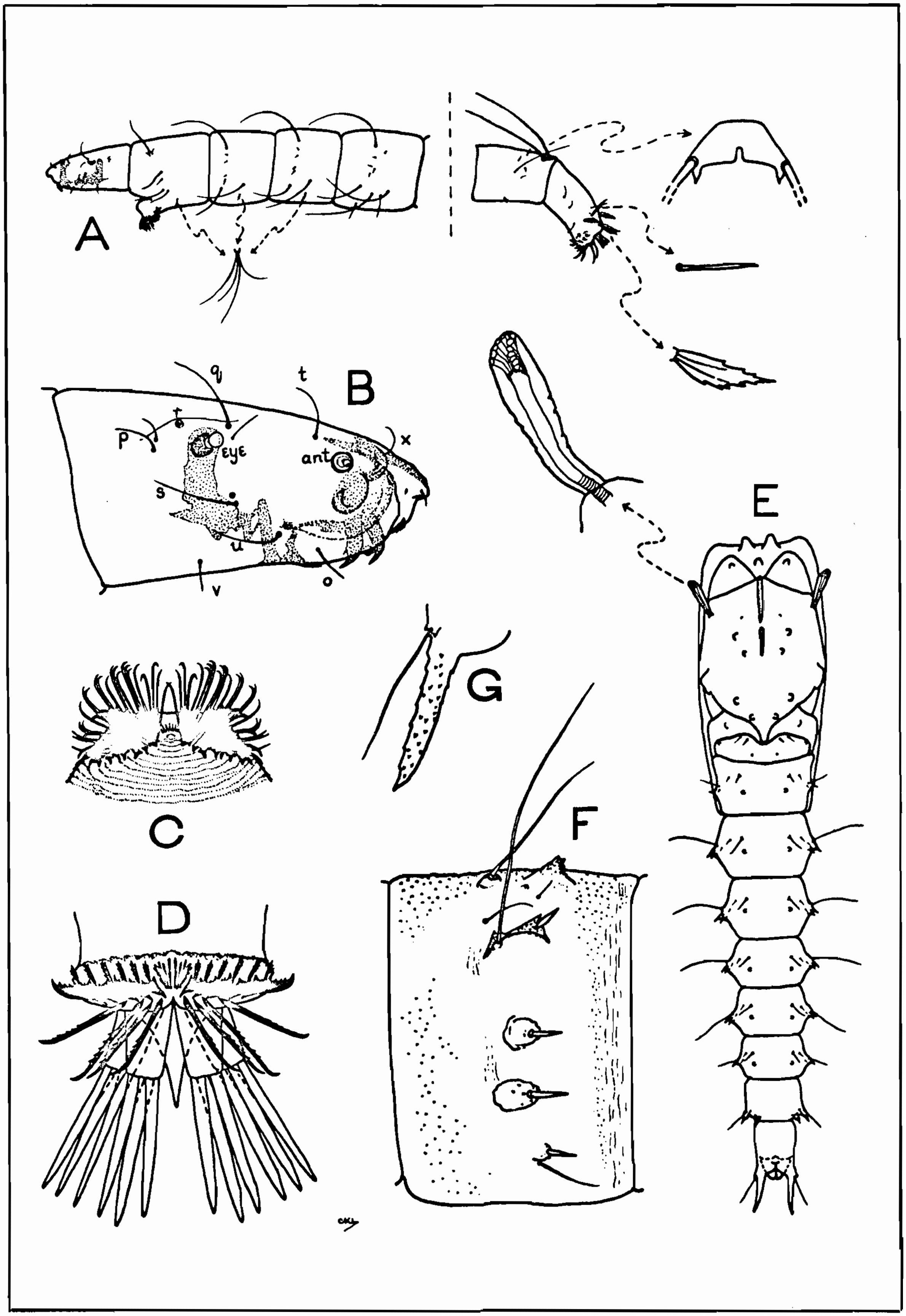
Head, yellow-brown with internal mouthpart skeleton dark brown; eyes, antennae and chaetotaxy as in Fig. 35B. HR 2.02 (2.00-2.05); OH/v 0.98 (0.94-1.02); qt/ts/sq 1.04 (1.o2-1.05): 1.27 (1.24-1.36): 1; tt/ant 0.48; qq/eyes 0.97 (0.95-1.00); qq/ss 0.61 (0.60-0.61); pp/qq 1.43; ss/uu 1.18 (1.17-1.18).

Body segments with chaetotaxy as shown (Fig. 35A). Prothorax with four pairs of very minute setae and four pairs of larger setae;

Fig. 35. *Trichohelea nicopina* n. sp.

- A-D, Fourth-instar larva:
  - A, Larva, lateral view
  - B, Head
  - C, Prothoracic pseudopod
  - D, Anal pseudopod
- E-G, Pupa:
  - E, Pupa, dorsal view
  - F, Fifth abdominal segment
  - G, Terminal process

Fig. 35



meso- and metathorax each with five pairs of minute setae and three pairs of long, fine setae. Prothoracic pseudopod (Fig. 35C) bearing three rows of hooks; on each side of the middle and anteriormost row consists of about 22 long, slender, hyaline hooks, the middle row of eight shorter, slender hyaline hooks and the posterior row of seven brownish, short hooks. Length and depth of prothoracic pseudopod in proportion of 1.18: 1.80: 1.

Abdominal segments 1-7 with similar chaetotaxy as shown (Fig. 35A) eac h segment with seven pairs of short, minute setae and four pairs of longer, slender, setae. Segments 8 and 9 with chaetotaxy as shown (Fig. 35A). Chaetae arising from sclerotized bar at posterior margin of penultimate segment extending to about end of last segment or slightly beyond. Posterior pseudopod (Fig. 35D) with two rows of hooks, five in the anterior row and four in the posterior row and six longitudinal ridges anterior to and lying between consecutive hooks of the anterior row. Both the stout short hooks of the anterior row and the slender long ones of the posterior row are serrated on the anterior edges. Cauda conical, rather short, bluntly pointed at tip. Anal blood gills four, each tripartite from basal third to tip.

Pupa.-

Length 2.70 mm. in female and 2.28 mm. in male.

Median head sclerite with three tubercles and lateral sclerites each with one tubercle bordered on inner edge by a minute circular marking. Cephalothorax about twice as long as greatest width (2.19: 1) in female and 2.18: 1 in male. Ratio of length of head to thorax 0.48 in ventral aspect and 0.27 in dorsal aspect in female and respectively 0.58 and 0.31 in male.

Thorax bearing on dorsum two median ridges anteriorly and five pairs of tubercles (Fig. 35E), none setigerous. Prothoracic horn (Fig. 35E) slender, imbricated in middle region and bearing at apex sixteen spiracular papillae in female and twelve in male; horn 4.73 and 6.00 as long as greatest width in female and male respectively; tracheal length to horn length 0.78 and 0.78 respectively in female and male.

Chaetotaxy on abdominal segments 3-7 similar except for shorter setae on anterior lateral tubercle in segment 7, each segment with four dorsal pairs, three lateral pairs and three ventral pairs of tubercles (Fig. 35F), segment 8 with two pairs dorsal, three pairs lateral and two pairs ventral tubercles. Chaetotaxy on other segments as illustrated (Fig. 35E). Terminal processes of last segment (Fig. 35E, Fig. 35G) rather short and their lateral setae about equal in length.

Cuticular armature very finely shagreened (Fig. 35F).

Adult Female.-

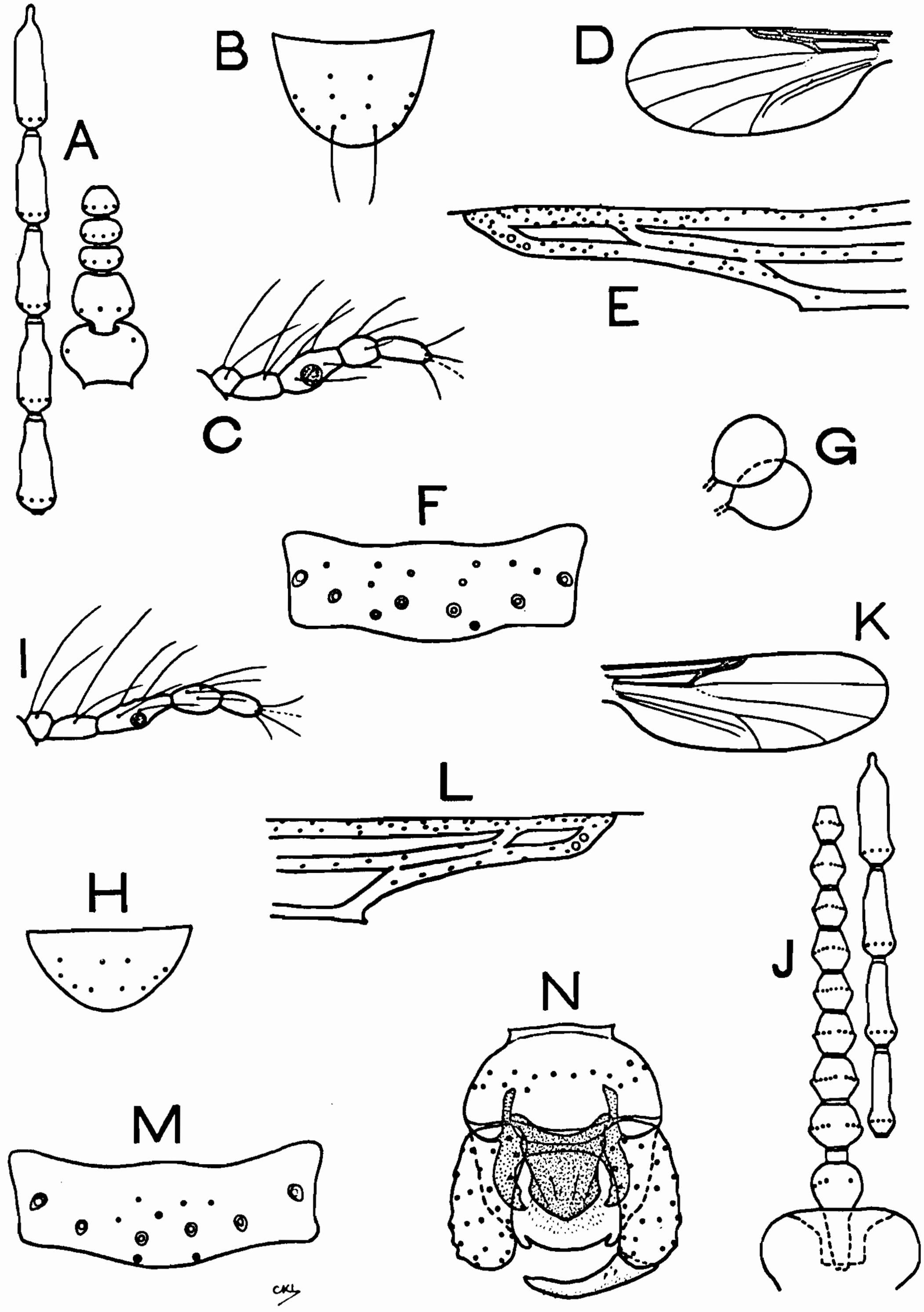
Length 1.65 mm. Wing (Fig. 36D) 0.75 x 0.33 mm.

Head with antennae and mouthparts light brown, eyes and pedicels dark brown to black; clypeus (Fig. 36B) with thirteen bristles. Antennae (Fig. 37A) with nine flagellar segments as in oligarthra Saunders (1956), first segment also indicating by its five sets of chaetae an amalgamation of the normal five segments; AR 3.45. Maxillary palp (Fig. 36C) with unusually stout fourth segment and bearing in middle of rather stout third segment a large, shallow sensory pit; PR 2.15; palp segments in proportion of 5: 9: 14: 8: 10.

Fig. 36. _Trichohelea_ _nicopina_ n. sp.

- A-G, Adult female:
  - A, Antenna
  - B, Clypeus
  - C, Maxillary palp
  - D, Wing
  - E, Anterior wing venation
  - F, Scutellum
  - G, Spermathecae
- H-N, Adult male:
  - H, Clypeus
  - I, Maxillary palp
  - J, Antenna
  - K, Wing
  - L, Anterior wing venation
  - M, Scutellum
  - N, Genitalia

Fig. 36



Thorax dark brown, with scutellar bristle arrangement as shown (Fig. 36F). Legs uniformly pale brown; TR 2.94 in fore leg, 3.06 in middle leg and 3.15 in hind leg; apical tibial comb with seven bristles.

Wings brown; CR 0.54. Venation: vLR 1.14: 1: 1.94; rs/r_1 1.87; first radial cell obliterated, second radial cell narrow; RR 1.04 (Fig. 36E); fmcu under about middle of second radial cell; m_{3+4}/ cu_1 1.69.

Abdomen dark brown on dorsum. Spermathecae (Fig. 36G) two, practically identical in shape and size and measuring 56.93 x 44.85 μ and 56.93 x 48.30 μ.

Adult Male.-

Length 1.74 mm. Wings (Fig. 36K) 0.81 x 0.29 mm. Color as in female.

Clypeus (Fig. 37H) with ten bristles; antennae (Fig. 36J) with usual thirteen flagellar segments; AR 0.94. Maxillary palp (Fig. 36I) slender, with fourth segment stout and third segment bearing small shallow sensory pit at about middle of segment; PR 2.73.

Thorax dark brown; scutellum with six large bristles (Fig. 36M). Legs uniformly brown with TR 2.63 in fore leg and middle leg and 3.16 in hind leg; apical tibial comb of hind leg with six bristles.

Wings brown; CR 0.48. Venation: vLR 1.12: 1: 1.73; rs/r_1 1.59; first radial cell obliterated, second radial cell moderately wide, shorter than first (0.72: 1) (Fig. 36L); fmcu under about end of r_1; m_{3+4}/cu_1 2.13.

Genitalia (Fig. 36N): sternite 9 shorter than wide (0.54:1), tergite 9 shorter than wide (0.63: 1); parameres with basimeres 2.38

times as long as wide and telomeres 4.42 times as long as wide; aedeagus broadly shield-shaped, with lateral lobed expansions; claspettes the usual curved, spoon-like structures, b/c/b in proportion of 0.61: 1: 0.61.

Holotype (fourth instar larva).-

Collected in watery detritus in apical leaf axils of pineapple plants at Wallace Way, Singapore, in May 1962. Deposited in Lyman Entomological Museum, Macdonald College, Quebec.

Paratypes.-

Collected from same habitat and locality; 2 larvae, 5 pupae, 2 females, 9 males and 31 assorted pupal exuviae, in personal collections.

This species is very close to *Forcipomyia* (*Trichohelea*) *oligarthra* Saunders (1956) in all its stages. The larva resembles that of *oligarthra* in general appearance but differs from the latter in possessing four pairs of long, and seven pairs of short hairs on abdominal segments 1-7 instead of four pairs of long and two pairs of short hairs. It also differs from *oligarthra* in the shorter stout setae flanking the cauda, in the shape of the sclerotized bar at the posterior margin of the penultimate segment and in the tripartite distal two-thirds of the four anal blood gills instead of the bipartite distal half in *oligarthra*.

The pupa of this species also resembles that of *oligarthra* but differs from the latter in having five pairs of tubercles on the dorsum of the thorax instead of three pairs. The female also resembles that of *oligarthra* in the reduced number of flagellar segments but differs in having a shallow sensory pit instead of a deep one in the third palpal segment.

The male of this species show no real difference in the structure of the genitalia from that of oligarthra.

nicopina also resembles very closely another pineapple-inhabiting species, Apelma brevis Johannsen (1927) from Hawaii, but differs from brevis in a number of characters. In the male of brevis the second palpal segment is "nearly as long as the third" but in nicopina the third is distinctly much longer than the second. In brevis the third palpal segment is broader than the following segment but in nicopina it is as broad or narrower than the following segment; the third palpal segment in brevis is "as long as the two succeeding segments taken together" but in nicopina the third segment is shorter than the last two taken together. In the male antenna brevis has the eleventh segment twice as long as the tenth but in nicopina the eleventh is about 2½ times as long as the tenth. Johannsen (1927) did not figure the male genitalia in his original description but Hardy (1960) has figured them. From Hardy's figures it is clear that the claspettes of brevis are not precisely H-shaped and are slender rather than stout, with spoon-shaped caudal lobes as in nicopina.

In the female of brevis Johannsen (loc. cit.) describes the second antennal segment as "nearly 1.5 times as long as broad". In the female of nicopina the second antennal segment is broader than long or about as broad as long.

The pupa of brevis also differs from that of this species in possessing two pairs of dorsal thoracic tubercles instead of four pairs.

Trichohelea grandis CHAN NEW SPECIES

Larva.-

Length of full grown fourth instar (Fig. 37A) 3.85 mm. Body cylindrical with only head flattened dorso-ventrally.

Head with eyes, antennae and setae as shown (**Fig.** 37B). p and q setae short. HR 1.99 (1.89-2.07); OH/v 0.97 (o.96-0.98); qt/ts/sq 1.26: 1.40: 1; tt/ant 0.54 (0.52-0.55); qq/eyes 0.84 (0.82-0.87); qq/ss 0.61 (0.58-0.65); pp/qq 1.40 (1.35-1.44); pq/qs/sp 1.41: 1: 1.61.

Body segments with chaetotaxy as shown (Fig. 37A). Prothorax bearing seven pairs of chaetae, two pairs longer than the rest; meso- and meta-thorax similar in chaetotaxy , each bearing eight pairs of setae, also two pairs longer than the others. Prothoracic pseudopod (Fig. 37C) with a row of about twelve hyaline curved hooks and many hyaline, long, fine hair-like hooklets beyond the row.

Abdominal segments 1-7 similar in chaetotaxy, each segment bearing two pairs of long setae and six pairs of shorter ones. Segments 8 and 9 with chaetotaxy as shown (Fig. 37A). Chaetae arising from sclerotized base at posterior margin of penultimate segment short, extending to about two-thirds of last segment. Posterior pseudopod (Fig. 37D) as in nicopina but with shorter cauda.

Pupa (Male only).-

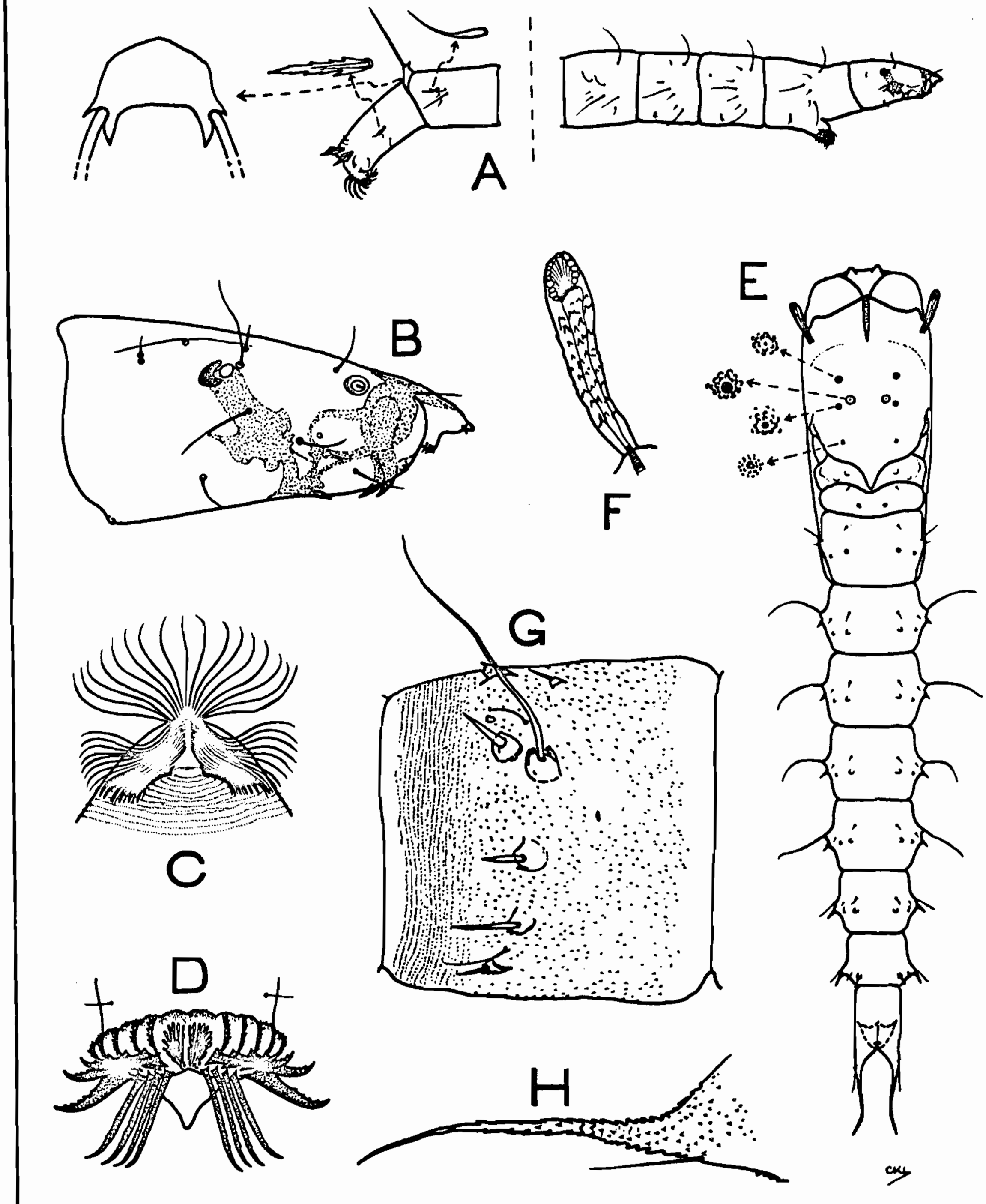
Length 2.76 mm.

Median head sclerite with two tubercles; lateral sclerites without tubercles. Cephalothorax more than twice as long as greatest width (2.48: 1); ratio of length of head to thorax 0.36 in ventral aspect and 0.26 in dorsal aspect.

Fig. 37. *Trichohelea grandis* n. sp.

A-D, Fourth-instar larva:
  A, Larva, lateral view
  B, Head
  C, Prothoracic pseudopod
  D, Anal pseudopod
E-H, Pupa:
  E, Pupa, dorsal view
  F, Prothoracic horn
  G, Sixth abdominal segment
  H, Terminal process

Fig. 37



Thoracic dorsum bearing a median ridge anteriorly and four pairs of minute, rosette-like tubercles (Fig. 37E). Prothoracic horn (Fig. 37F) narrow, imbricated except basal and distal ends and bearing about 14 spiracular papillae; horn length 5.50 times as long as its greatest width; tracheal length to horn length 0.82.

Chaetotaxy on abdominal segments 3-7 similar except for shorter lateral setae on segment 7; each segment with four pairs dorsal, three pairs lateral and two pairs ventral tubercles (Fig. 37G). Chaetotaxy on other abdominal segments as illustrated (Fig. 37A).

Cuticular armature finely shagreened (Fig. 37G).

Adult Female.-

Length 1.43 mm. Wing (Fig. 38C) 0.72 x 0.30 mm.

Head with antennae and mouthparts light brown; eyes and pedicels dark brown. Antennae (Fig. 38B) with the usual thirteen flagellar segments, segments 2-6 compressed; AR 1.46 (1.37-1.55). Maxillary palp (Fig. 38A) with stout segment 3 bearing capitate sensilla in somewhat triangular shallow sensorium; PR 2.14; last segment longer than preceding; segments in proportion of 8: 9: 20: 14: 19.

Thorax dark brown, with scutellar bristle arrangements as shown (Fig. 38E). Legs uniformly light brown with TR 2.84 in fore leg, 2.79 in middle leg and 3.27 in hind leg.

Wings brown. CR 0.52. Venation: vLR 1.15: 1: 1.92; rs/r_1 1.97; first radial cell obliterated, second radial cell rather wide, slightly longer than first (1.30:1) (Fig. 38D); fmcu under about end of r_1; m_{3+4}/cu_1 2.00.

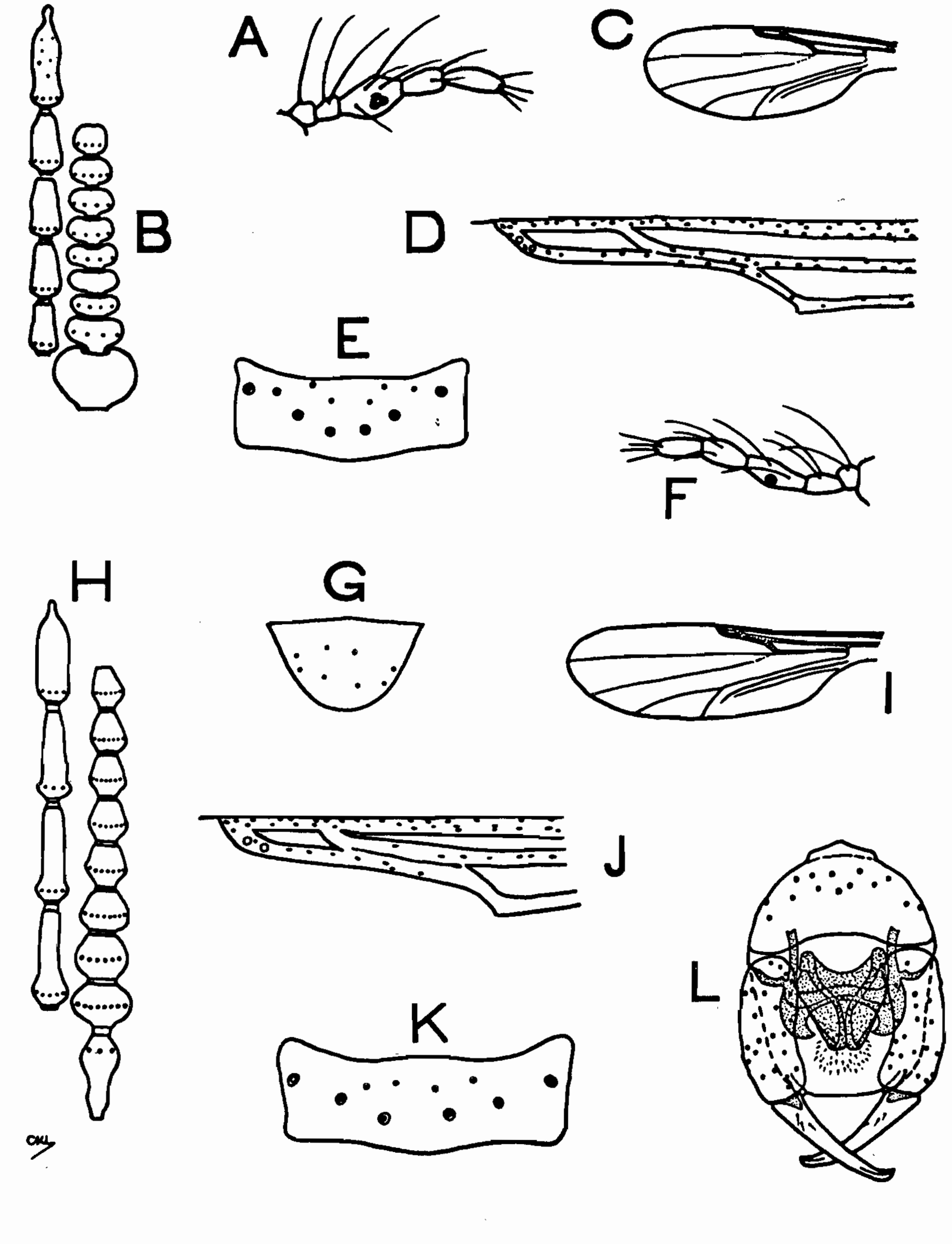
Adult Male.-

Length 1.49 mm. Wing (Fig. 38I) 0.80 x 0.27 mm. Color as in

Fig. 38. <u>Trichohelea</u> <u>grandis</u> n. sp.

A-E, Adult female:
  A, Maxillary palp
  B, Antenna
  C, Wing
  D, Anterior wing venation
  E, Scutellum
F-L, Adult male:
  F, Maxillary palp
  G, Clypeus
  H, Antenna
  I, Wing
  J, Anterior wing venation
  K, Scutellum
  L, Genitalia

Fig. 38



female.

Clypeus (Fig. 38G) with eight bristles. Antennae (Fig. 38H) with segments 3-5 wider than long and the remaining segments longer than wide; AR 0.89. Maxillary palp (Fig. 38F) slender, with segment 4 as wide as segment 3, the latter bearing a small sensorium at middle region; segments in proportion of 4: 8: 12: 10: 9; PR 2.67.

Thorax dark brown; scutellum with six large and four small bristles (Fig. 38K); legs brown; TR 2.62 (2.56-2.68) in fore leg, 2.52 (2.32-2.72) in middle leg and 2.85 (2.79-2.92) in hind leg; hind tibial comb with six tibial spines.

Wings brown; CR 0.47. Venation: vLR 1.12: 1: 1.83; rs/r_1 1.61; first radial cell obliterated, second radial cell small, rather narrow, 0.70 times as long as first (Fig. 38J); fmcu under about end of costa; m_{3+4}/cu_1 2.15.

Genitalia (Fig. 38L): ninth sternite 0.56 (0.55-0.57) times as long as wide, ninth tergite 0.78 (0.75-0.80) times as long as wide; parameres with basimeres 2.88 (2.80-2.95) times as long as wide and telomeres 4.75 (4.33-5.17) times as long as greatest width at base; aedeagus shield-shaped, more heavily sclerotized along edges and cup-shaped inner edges of each half, slightly shorter than wide (0.89 (0.88-0.89): 1); claspettes the usual spoon-shaped structure but with spoon-shaped caudal lobes rather short, b/c/b 0.68 (0.65-0.71): 1: 0.68 (0.65-0.71).

Holotype (pupa). Collected in watery detritus in leaf axils of a species of aroid plant (Colocasia species) about ten feet tall with large cordate-shaped leaves at Wallace Way, Singapore, in May 1962.

Paratypes.-

Collected from same habitat and locality; 9 larvae, 2 pupae, 1 male and 1 female deposited in the Department of Zoology, University of Singapore.

This species closely resembles Forcipomyia (Apelma) comis Johannsen (1932) from Sumatra, Java and Bali whose larvae were obtained from water in leaf axils of two species of Colocasia. Johannsen did not describe nor figure the early stages of comis and his original description of the adults is insufficiently quantitative to allow for comparisons with grandis. Moreover, his figure of the male genitalia of comis does not show the claspettes. The aedeagus of comis does not show any essential difference from that of grandis . The latter however differs from comis in the smaller AR of 0.89 in the male. Johannsen's statement "antennal segments 2-9 combined over 0.8 as long as 10-14 combined" shows that the AR of comis at its greatest is 1.25 since the AR in the present terminology is taken as the length of segments 11-14 over that of segments 2-10. Thus the AR of comis must be above 1.0 and at most 1.25. The hind TR of this species is also larger than that of comis (2.85 to 2.60).

Although the larval habitats of the two species are roughly similar and would suggest identity, it is best to designate this species as new pending examination of the immature stages). In doing so the writer is not creating a precedence since several closely related species in this genus, namely oligarthra, nicopina and brevis are known to share in the immature stages the same kind of habitat, in pineapple leaf axils.

Species described in all stages.-

antiguensis (Saunders) (1956); early stages in epiphytic bromeliads in Antigua, W. Indies: Can. J. Zool. 34: 700

brevis Johannsen (1927); immature stages in water in pineapple leaf axils in Hawaii: Proc. Entomol. Soc. Washington, 29: 205

bromelicola Lutz (1914); early stages from small bromeliads on rocks in Rie Bay. Saunders (1924); Parasitology, 17: 263

caribbeana (Saunders) (1956); immature stages in epiphytic bromeliads in W. Indies (Trinidad); Can. J. Zool. 34: 696

comis Johannsen (1932); early stages in leaf axils of Colocasia species in Sumatra, Java and Bali; Arch. Hydrobid. 11(9):409

crinume Tokunaga (1934); (as Dasyhelea crinume); early stages in leaf bases of shore plant Crinim asiaticum var. japonicum (Amaryllidaceae), Japan. Philippine Journ. Sci. 53: 469

edwardsi Saunders (1925); early stages in terrestrial bromeliads in S. America (Brazil); Parasitology 17: 260

jocosa (Saunders) (1956); early stages in terrestrial Bromelia pinguin and pineapple in Trinidad, W. Indies. Can. J.Zool. 34: 701

keilini Saunders (1925); early stages from terrestrial bromeliads in S. America (Brazil); Parasitology 17: 265

magna Saunders (1925); early stages from terrestrial bromeliads in S. America (Brazil); Parasitology, 17: 266

oligarthra (Saunders) (1956); early stages in leaf axils of terrestrial bromeliads Bromelia pinguin in Puerto Rico; Can. J. Zool. 34: 698

Other species described in adult stages.-

auroniteus Kieffer (1919); Ann.Mus. Nat. Hung. 17: 64

hamaticauda Tokunaga (1959); Insects of Micronesia 12(3); 212

sabroskyi Tokunaga (1959); Insects of Micronesia 12(3): 211

tsutsumii (Tokunaga) (1960); Akitu Kyoto 9: 76

J. GENUS PTEROBOSCA MACFIE (1932)

Type species aeschnosuga (De Meijere) (1923)

DIAGNOSIS

The following diagnosis is taken from Tokunaga's (1959) "Insects of Micronesia".

"Adult Female.-

Basal flagellar segments of antenna subspherical or discoidal; distal six or seven flagellar segments elongate. Maxillary palp distinctly five-segmented. Empodia of legs very large, broad and with radial structure; claws present or absent; hind TR 3.0 or more; scales of legs absent. Wings unmarked, without scale-like hairs, with macrotrichia moderately dense as in Lasiohelea; costal vein little or distinctly beyond middle of wing, second radial cell usually open, but sometimes obliterated, as long as, or a little longer than first radial cell; first radial cell almost closed or slit-like, One or two spermathecae."

Female of known species mainly ectoparasitic on Odonata and rarely on lacewing flies. Males and immature stages unknown.

Species described.-

aeschnosuga (De Meijere) (1923); Tijdschr. Entomol. 66: 137
Macfie, (1932); Tijdschr. Entomol. 15: 267

adhesipes (Macfie) (1932); Tijdschr. Entomol. 75: 270

aerobates Macfie (1936); Proc. Roy. Entomol. Soc. London (B) 5: 64

ariel Macfie (1932); Tijdschr. Entomol. 75: 275

asahinai (Tokunaga) (1962); Pacific Insects 4(1): 188

chrysopae (Tokunaga) (1959); Insects of Micronesia 12(3): 235

esakii Tokunaga (1940); Philippine Jour. Sci., 71(2): 210

feminae Tokunaga (1940); Tenthredo 3(2): 168
Tokunaga and Murachi (1959); Insects of Micronesia 12(3): 230

fidens Macfie (1936); Proc. Roy. Entomol. Soc. London 5(12): 227

fusicornis (Coquillett) (1905); Jour. N.Y. Entomol. Soc. 13: 63

incubans Macfie (1937); Proc. Roy. Entomol. Soc. London (B) 6: 111

latipes Macfie (1936); Proc. Roy. Entomol. Soc. London (B) 5: 227

lairdi Wirth (1956); Ann. Entomol. Soc. Am. 49: 363

mollipes Macfie (1932); Tijdschr. Entomol. 75: 272

odonatiphila Macfie (1932); Tijdschr. Entomol. 75: 274

paludis Macfie (1936); Proc. Roy. Entomol. Soc. London (B) 5: 63

tokunagai Oka and Asahina (1948); Mushi 18: 107
Tokunaga (1960); Akitu 9: 75
Tokunaga (1962); Pacific Insects 4(1): 127

K. GENUS PARAPTEROBOSCA HARANT AND HUTTEL (1951)

Type species anthropophila Harant and Huttel (1951)

DIAGNOSIS

Adult Female.-

Basal flagellar segments of antenna subspherical to discoidal; distal six segments elongate. Maxillary palp four-segmented, first two segments completely fused, segment 3 (second segment in palp) with large sensorium. Legs testaceous[1], without ornamentation, hind TR 2.2; empodia well developed but not very broad, large and with radial structure as in Pterobosca; claws simple. Wings unmarked, with

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[1] Term used by Harant and Huttel in their original description to mean presumably "brown and sclerotized".

macrotrichia moderately dense, and with two rows of macrotrichia on posterior fringe of wing; costa distinctly beyond middle of wing, first and second radial cells obliterated; anterior border just beyond tip of costa with a clear spot. One spermatheca, subglobular.

Females of the species listed hereunder, the only species recorded, are blood-suckers of man in Africa. Males and immature stages are unknown.

Parapterobosca anthropophila Harant and Huttel, (1951);
Ann. Parasitol. 26: 468

The exact systematic position of Parapterobosca and Pterobosca will eventually be determined when immature stages and males are discovered. Their present generic status is temporary and requires confirmation. The many morphological similarities between them suggest that the genus Parapterobosca is in all probability a subgenus of Pterobosca although it is differentiated from the latter by its man-biting habit and by the much smaller hind tarsal ratio of 2.2.

VII. GEOGRAPHICAL DISTRIBUTION

As pointed out by Kendeigh (1961), the best system of geographic faunal divisions yet devised is that given by Sclater (1858), modified by Huxley (1868) and extended by Wallace (1876). Bartholomew *et al.* (1911) in their "Atlas of Zoogeography" have also adopted Wallace's regional divisions since Wallace's (1876) great work treats zoogeography very exhaustively, taking into consideration all the classes of vertebrate animals and also certain invertebrates. Wallace's zoogeographical regions, based primarily on the distribution of vertebrates, have received some minor changes for insects, but there still remain disagreements on some of these changes (Gressitt, 1958). For convenience, Wallace's scheme is followed for the geographical distribution of the Forcipomyiinae.

The geographical distribution of the Forcipomyiinae has not been discussed or compiled to date and it is considered worthwhile to present at this time a concise account of the distribution of the subfamily as it is now known, the object being to throw light on the phylogeny of the group.

The geographical distribution of all established and known genera and subgenera of the Forcipomyiinae is worked out and listed below and also summarized in Table 1. It has not been possible to include all known species in all the genera and subgenera, especially those of the large subgenus *Forcipomyia* s. str. and the genus *Atrichopogon* for which the many synonymies are not properly worked out as yet. Species whose identification is doubtful or not confirmed are headed with a question mark.

In compiling the list of species in the different geographical regions the following major contributions were consulted:

1. Carter, H.F. 1919.
   West African Ceratopogonidae.
   Ann. Trop. Med. Parasitol. 12:289-302

2. Coquillett, D.W. 1905.
   Nematocerous Diptera from N. America.
   N.Y. Entomol. Soc. 13:56-69

3. Edwards, F.W. 1926.
   British biting midges.
   Trans. Roy. Entomol. Soc. London 74:389-462

4. Ewen, A.B. and Saunders, L.G. 1958.
   Atrichopogon (revision).
   Can. J. Zool. 36:671-724

5. Hardy, D.E. 1960.
   Ceratopogonidae (Hawaii).
   Univ. Hawaii Press, Honolulu 10:165-187

6. Johannsen, O.A. 1932.
   Ceratopogonidae (Malayan Subregion of the
   Dutch East Indies).
   Arch. Hydrobiol. 9:403-448

7. Johannsen, O.A. 1943.
   A generic synopsis of the Ceratopogonidae
   (Heleidae) of the Americas, a bibliography,
   and a list of the North American species.
   Ann. Entomol. Soc. Am. 36:761-791

8. Lee, D.J. and Reye, E.J. 1954.
   Australasian Ceratopogonidae (*Lasiohelea*).
   Proc. Linn. Soc. N.S.W., Sydney 79(5/6):233-246

9. Macfie, J.W.S. 1932.
   Biting midges (New Zealand).
   Ann. Trop. Med. Parasitol. 26:23-53

10. Macfie, J.W.S. 1932.
    Ceratopogonidae from wings of dragonflies.
    Tijdschr. Entomol. 75:265-283

11. Macfie, J.W.S. 1934.
    Ceratopogonidae (Malaya).
    Ann. Trop. Med. Parasitol. 28:177-195

12. Macfie, J.W.S. 1934.
    Ceratopognidae (Sumatra).
    Tjidschr. Entomol. 77:202-231

13. Macfie, J.W.S. 1935.
    Ceratopogonidae (Society Is.).
    Bull. Bishop Mus. 113:75-80

14. Macfie, J.W.S. 1935.
    Ceratopogonidae (Marquesas Is.).
    Bull. Bishop Mus. 114:93-105

15. Macfie, J.W.S. 1937.
    Ceratopogonidae (Trinidad).
    Ann. Mag. Nat. Hist. 20(10):1-18

16. Macfie, J.W.S. 1939.
    Ceratopogonidae (New Guinea).
    Proc. Linn. Soc. N.S.W., Sydney 64:356-368

17. Macfie, J.W.S. 1939.
    Ceratopogonidae (Brazil).
    Rev. Entomol. Rio de Janeiro 10:137-219; 481-482

18. Macfie, J.W.S. 1940.
    Ceratopogonidae (British Guiana, Trinidad).
    Proc. Roy. Entomol. Soc. London (B) 9:179-195

19. Macfie, J.W.S. 1940.
    Ceratopogonidae.
    Ann. Trop. Med. Parasitol. 34:13-30

20. Macfie, J.W.S. 1943.
    Ceratopogonidae (Egypt).
    Proc. Roy. Entomol. Soc. London (B) 12:145-159

21. Saunders, L.G. 1924.
    Forcipomyia s. str.
    Parasitology 16:164-213

22. Saunders, L.G. 1956.
    Revision of the genus Forcipomyia.
    Can. J. Zool. 34:657-705

23. Saunders, L.G. 1959.
    Forcipomyiinae (Proforcipomyia, Thyridomyia).
    Can. J. Zool. 37:33-51

24. Saunders, L.G. 1964.
    Forcipomyiinae (Lasiohelea complex).
    Can. J. Zool. 42:463-482

25. Tokunaga, M. 1940.
Biting midges (Japan).
Tenthredo 3:92-94

26. Tokunaga, M. 1962.
Biting midges (Ryukyu Is.).
Pacific Insects 4(1):153-217

27. Tokunaga, M. and Murachi, E.K. 1959.
Ceratopogonidae (Micronesia).
Bishop Museum, Insects of Micronesia 12(3):103-434

28. Wirth, W.W. 1952.
Heleidae of California.
Univ. Calif. (Berkeley) Publ. Entomol. 9:95-266

29. Wirth, W.W. 1956.
Biting midges ectoparasitic on insects.
Ann. Entomol. Soc. Am. 49:356-364

GENUS *PROFORCIPOMYIA* SAUNDERS

PALEARCTIC

A. European

crassipes (Winnertz) (1852); England

titillans (Winnertz) (1852); England

B. Manchurian

formosana (Kieffer) (1916); Ryukyu Is.

? *ishigakia* (Tokunaga) (1962); Ryukyu Is.

sauteri (Kieffer) (1912); Ryukyu Is.

yapensis (Tokunaga and Murachi) (1959); Ryukyu Is.

yoshimurai (Tokunaga) (1940); Kyoto

ETHIOPIAN

A. West African

ingrami (Carter) (1919); Accra, Gold Coast

ORIENTAL

A. Indo-Chinese

formosana (Kieffer) (1916); Taiwan

sauteri (Kieffer) (1912); Taiwan

B. Indo-Malayan

clara Chan (1965); Singapore

ingrami (Carter) (1919); Indonesia, Malaya

pennielongata Chan (1965); Singapore

AUSTRALIAN

A. Austro-Malayan

sauteri (Kieffer) (1912); New Guinea, New Britain

B. Polynesian

bituberculifera (Tokunaga) (1959); Micronesia

ingrami (Carter) (1919); Hawaii, Samoa, Marquesas Is.

palikuensis (Hardy) (1960); Hawaii

sauteri (Kieffer) (1912); Micronesia

yapensis (Tokunaga and Murachi) (1959); Micronesia

NEOTROPICAL

A. Brazilian

bromeliae (Saunders) (1956); Brazil (Rio de Janeiro, Pernambuco)

falcifera (Saunders) (1959); Trinidad

longispina (Saunders) (1956); Brazil (Rio de Janeiro)

mortuifolii (Saunders) (1959); Trinidad

setigera (Saunders) (1959); Trinidad

spatulifera (Saunders) (1956); Santos (Brazil)

B. Mexican

sp. B (Saunders, 1959); Costa Rica

C. Antillean

ingrami (Carter) (1919); B.W.I.

sp. A (Saunders, 1959); Grenada

NEARCTIC

A. Californian

wirthi (Saunders) (1956); California

B. Rocky Mountain

calcarata (Coquillett) (1905); Mexico

calcarata var. sonora (Wirth) (1952); Nevada, New Mexico, Utah

C. Alleghany

calcarata (Coquillett) (1905); Florida

calcarata var. sonora (Wirth) (1952); Washington

fusicornis (Coquillett) (1905); Florida, Maryland

hirtipennis (Malloch) (1915); Illinois

johannseni (Thomsen) (1935); New York

longitarsis (Malloch) (1915); Illinois

GENUS CALOFORCIPOMYIA SAUNDERS

PALEARCTIC

Manchurian

takahashii (Tokunaga) (1940); Ryukyu Is.

ETHIOPIAN

? auripes (Macfie) (1924); Gold Coast

ORIENTAL

Indo-Chinese

takahashii (Tokunaga) (1940); Taiwan

AUSTRALIAN

Austro-Malayan

squamianulipes (Tokunaga and Murachi (1959); New Guinea

Polynesian

squamianulipes (Tokunaga and Murachi) (1959); Micronesia

NEOTROPICAL

Brazilian

caerulea (Saunders (1956); Rio de Janeiro (Brazil)

varicolor (Saunders) (1956); Rio de Janeiro (Brazil)

NEARCTIC

Alleghany

pluvialis (Malloch) (1923); Virginia

GENUS METAFORCIPOMYIA SAUNDERS

NEOTROPICAL

Brazilian

cerifera (Saunders) (1956); Rio de Janeiro (Brazil)

GENUS FORCIPOMYIA MEIGEN

SUBGENUS SCHIZOFORCIPOMYIA CHAN

PALEARCTIC

Manchurian

? fuscimanus (Kieffer) (1921); Ryukyu Is.

ORIENTAL

Indo-Chinese

? fuscimanus (Kieffer) (1921); Taiwan

Indo-Malayan

lerouxi Chan (1965); Singapore

AUSTRALIAN

Polynesian

? fuscimaculata (Hardy) (1960); Hawaii

? fuscimanus Kieffer (1921); Micronesia

? penniornata (Tokunaga) (1959); Micronesia

NEARCTIC

Canadian

one species (unidentified) ... Chan (1965); Quebec

SUBGENUS FORCIPOMYIA S. STR. MEIGEN

PALEARCTIC

European

bipunctata (Linnaeus) (1767); England

braueri (Wasmann) (1893); England

brevipennis (Macquart) (1826); England

ciliata (Winnertz) (1852); England

corticis (Kieffer) (1911); Germany

flavipubens Goetghebuer (1927); Belgium

fuliginosa (Meigen) (1818); Finland, Germany, Scotland, Belgium

nigra (Winnertz) (1852); England

picea (Winnertz) (1852); England

pulchrithorax Edwards (1924); England

radicicola Edwards (1924); England

raleighi Macfie (1938); England

sanguinolenta Kieffer (1926); Germany

sphagnophila Kieffer (1926); Germany

squamigera Kieffer (1929); Sweden

Mediterranean

aegyptius Kieffer (1925); Egypt

alfierii Kieffer (1925); Egypt

brachypetrolata Vimmer (1928); Palestine

egypti Macfie (1924); Egypt

flavicincta Abreau (1918); Canary Is.

flavomaculata Vimmer (1928); Palestine

fulvescens Abreau (1918); Canary Is.

hathor Kieffer (1925); Egypt

imaculata Vimmer (1928); Palestine

isis Kieffer (1925); Egypt

litoralis Abreau (1918); Canary Is.

nilotheres Macfie (1924); Egypt

ochracea Vimmer (1928); Palestine

osiris Kieffer (1925); Egypt

palmensis Abreau (1918); Canary Is.

praecincta Abreau (1918); Canary Is.

pulcherrima Abreau (1918); Canary Is.

sate Kieffer (1925); Egypt

urnigera Kieffer (1925); Egypt

Manchurian

abdominalis Tokunaga (1940); Japan

akizukii Tokunaga (1940); Japan

albiradialis Tokunaga (1940); Ryukyu Is., Honshu, Kokkaido angelicae Tokunaga (1940); Japan

anguliforceps Tokunaga (1940); Japan

annulipes Tokunaga (1940); Japan

arcigera Kieffer (1922); Ryukyu Is.

astyla Tokunaga (1940); Japan

atomaria Tokunaga (1940); Japan

binigrimaculata Tokunaga (1940); Kyoto

bipunctata (Linnaeus) (1767); Japan

breviforceps Tokunaga (1940); Japan

brevipennis (Macquart) (1826); Japan

distinctiscuta Tokunaga (1962); Ryukyu Is.

edgari Tokunaga and Murachi (1959); Ryukyu Is.

esakiana Tokunaga (1940); Ryukyu Is.

fascicomis Tokunaga (1962); Ryukyu Is.

formosae (Kieffer) (1922); Ryukyu Is.

fuliginosa (Meigen) (1818); Ryukyu Is.

fuscimanus Kieffer (1921); Japan

hikosanensis Tokunaga (1940); Ryukyu Is., Kyushu

kitasirakawae Tokunaga (1940); Japan

kyotensis Tokunaga (1940); Japan

longimaculata Tokunaga (1940); Japan

longiradialis Tokunaga (1940); Japan

maculipennis Tokunaga (1940); Japan

magnipunctata Tokunaga (1940); Japan

manchuriensis Tokunaga (1941); Manchuria

metatarsis Tokunaga (1940); Japan

monilis Tokunaga (1962); Ryukyu Is.

nibleyi Tokunaga (1962); Ryukyu Is.

subauronitens Tokunaga (1940); Japan

subnigra Tokunaga (1940); Japan

takagii Tokunaga (1941); Manchuria

vittata Tokunaga (1940); Japan

yamauchii Tokunaga (1940); Japan

yoshimurai Tokunaga (1940); Japan

ETHIOPIAN

East African

biannulata Ingram and Macfie (1924); Nyasaland

fuliginosa (Meigen) (1818); Nyasaland

West African

apicalis Goetghebuer (1935); Belgian Congo

ashantii Ingram and Macfie (1924); Gold Coast

atripennis Goetghebuer (1935); Belgian Congo

atrosetosa Goetghebuer (1935); Belgian Congo

auripes Ingram and Macfie (1924); Gold Coast

auripila Goetghebuer (1935); Belgian Congo

biannulata Ingram and Macfie (1924); Gold Coast, Nigeria

bicolorata Goetghebuer (1935); Belgian Congo

congolensis Goetghebuer (1933); Belgian Congo

curtimana Goetghebuer (1935); Belgian Congo

elongata Goetghebuer (1935); Belgian Congo

exigua Ingram and Macfie (1924); Gold Coast

flavicoxis Goetghebuer (1935); Belgian Congo

flavopilasella Goetghebuer (1933); Belgian Congo

fuliginosa (Meigen) (1818); Gold Coast, Liberia, French Cameroons, Belgian Congo, Nigeria *grata* Goetghebuer (1935); Belgian Congo

griseipluma Goetghebuer (1935); Belgian Congo

grisescens Goetghebuer (1935); Belgian Congo

guttatula Goetghebuer (1935); Belgian Congo

hirsuta Ingram and Macfie (1924); Gold Coast

inornatipennis var. *ornaticrus* Ingram and Macfie (1924; Gold Coast

kisantuensis Goetghebuer (1933); Belgian Congo

lepidota Ingram and Macfie (1924); Gold Coast

longiventris Goetghebuer (1935); Belgian Congo

lulengaensis Goetghebuer (1935); Belgian Congo

macronyx Goetghebuer (1933); Belgian Congo

marginella Goetghebuer (1935); Belgian Congo

melanchroa Ingram and Macfie (1924); Gold Coast

multiguttata Goetghebuer (1935); Belgian Congo

nigeriensis Ingram and Macfie (1924); Gold Coast

nigerrima Goetghebuer (1933); Belgian Congo

nigricosta Goetghebuer (1935); Belgian Congo

nigricoxis Goetghebuer (1935); Belgian Congo

nigrotibialis Ingram and Macfie (1924); Gold Coast

pampoikila Ingram and Macfie (1924); Gold Coast

quatuorguttata Goetghebuer (1935); Belgian Congo

rufula Goetghebuer (1935); Belgian Congo

scitula Goetghebuer (1935); Belgian Congo

squamipennis Ingram and Macfie (1924); Gold Coast

superata Goetghebuer (1935); Belgian Congo

thripsiformis Goetghebuer (1935); Belgian Congo

tigripes Ingram and Macfie (1924); Gold Coast trimaculata Goetghebuer (1935); Belgian Congo

variegata Goetghebuer (1933); Belgian Congo

venusta Ingram and Macfie (1924); Gold Coast

vicina Goetghebuer (1935); Belgian Congo

ORIENTAL

Indian

annandalei Edwards (1932); Barkuda Is.

Ceylonese

fuliginosa (Meigen) (1818); Ceylon

Indo-Chinese

arcigera Kieffer (1922); Taiwan

brachytomus Kieffer (1922); Taiwan

despecta Kieffer (1922); Taiwan

esakiana Tokunaga (1940); Thailand

formosae (Kieffer) (1922); Taiwan

formosana Kieffer (1916); Taiwan

fuliginosa (Meigen) (1818); Taiwan

lagonigera Kieffer (1922); Taiwan

longitarsis Tokunaga (1940); Taiwan

miricornis Kieffer (1916); Taiwan

takahashii Tokunaga (1940); Taiwan

Indo-Malayan

excellens Johannsen (1932); Java, Sumatra

fuliginosa (Meigen) (1818); Java, Sumatra, Malaya, Borneo

intonsa Chan (1965); Singapore

mira Johannsen (1932); Java

punctipes Edwards (1928); Malaya

securis Chan (1965); Singapore

simulans Johannsen (1932); Sumatra

subtilis Johannsen (1932); Java

swezeyanaadfinis Chan (1965); Singapore

AUSTRALIAN

Austro-Malayan

esakiana Tokunaga (1940); New Guinea

fuliginosa (Meigen) (1818); New Guinea

Australian

fuliginosa (Meigen) (1818); New South Wales

Polynesian

claggi Tokunaga (1959); Micronesia

edgari Tokunaga and Murachi (1959); Micronesia

esakiana Tokunaga (1940); Micronesia

fascicauda Tokunaga (1940); Micronesia

flavitibialis Tokunaga and Murachi (1959); Micronesia

fuliginosa (Meigen) (1818); Samoa, Fiji, Marquesas Is. Tahiti

gressitti Tokunaga and Murachi (1959); Micronesia

guamensis Tokunaga and Murachi (1959); Micronesia

ornata Tokunaga (1940); Micronesia

penniornata Tokunaga and Murachi (1959); Micronesia

punctipes Edwards (1928); Micronesia, Samoa

subspadicifascia Tokunaga and Murachi (1959); Micronesia

swezeyana Tokunaga and Murachi (1959); Micronesia

tuthilli Tokunaga (1959); Micronesia

New Zealand

antipodum Macfie (1932); Waiho, Otira, Christchurch, Kaitouna, Kaikoura, Aniseed Valley, Ohakune, Nelson

cooki Macfie (1932); Days Bay, Khandallah, Kaikoura, Nelson

desurvillei Macfie (1932); Mt. Dun

tapleyi Ingram and Macfie (1932); Welton's Bush, Waiho, Lake Brunner, Christchurch, Kaitoura, Purau Creek, Kaikoura, Nelson

tasmani Macfie (1932); Khandallah, Wellington, Purau Creek, Kaikoura, Aniseed Valley, Nelson Lake Rotoroa.

NEOTROPICAL

Chilean

fuliginosa (Meigen) (1818); South Chile, Patagonia, Argentina Galapagos Is.

Brazilian

annulatipes Macfie (1939); Brazil

argenteola Macfie (1939); Rio de Janeiro (Brazil)

brasiliensis Macfie (1939); Brazil

discoloripes Macfie (1939); Brazil

dubia Macfie (1939); Brazil

eukosoma Macfie (1939); Brazil

fuliginosa (Meigen) (1818); Brazil, Trinidad, French Guiana Paraguay, Ecuador

furcifera Macfie (1940); Brazil

insigniforceps Macfie (1939); British Guiana

ixodoides (Fiebrig-Gertz) (1928); Paraguay

kuanoskeles Macfie (1939); Brazil

lacrimatorii Macfie (1939); Brazil

narthekophora Macfie (1939); Brazil

<u>nigrescens</u> Macfie (1939); Brazil

<u>obercrombyi</u> Macfie (1938); Trinidad

<u>obesa</u> Lima (1928); Brazil

<u>ornatipennis</u> Macfie (1939); Brazil

<u>pictoni</u> Macfie (1938); Trinidad

<u>quasiingrami</u> Macfie (1939); Brazil

<u>raleighi</u> Macfie (1938); British Guiana, Trinidad

<u>tenniforceps</u> Macfie (1939); Brazil

<u>universicula</u> Macfie (1939); Brazil

<u>Mexican</u>

<u>crudelis</u> (Mayer) (1937); Costa Rica

<u>fuliginosa</u> (Meigen) (1818); Costa Rica

Antillean

<u>fuliginosa</u> (Meigen) (1818); St. Vincent Is., Puerto Rico, Cuba, Jamaica, Dominican Republic, Bahamas, Trinidad

<u>genualis</u> Loew (1865); Cuba

NEARCTIC

Californian

<u>bipunctata</u> (Linnaeus) (1767); California

<u>brevipennis</u> (Macquart) (1826); California

<u>cilipes</u> (Coquillett) (1905); California

<u>christiansoni</u> Wirth and Hubert (1960); California

<u>desertensis</u> Wirth and Hubert (1960); California

<u>fuliginosa</u> (Meigen) (1818); California

<u>hurdi</u> Wirth (1952); California

<u>macswaini</u> Wirth (1952); California

<u>occidentalis</u> Wirth (1952); California

quatei Wirth (1952); California

squamipes (Coquillett) (1902); California

texana texana (Long) (1902); California

texana simulata Walley (1932); California

townesi Wirth (1952); California

Rocky Mountain

bipunctata (Linnaeus) (1767); Oklahoma, Texas, New Mexico, Utah

brevipennis (Macquart) (1826); Colorado, Texas, Oklahoma, North Dakota, Nevada

cilipes (Coquillett) (1900); Oregon, Utah

cinctipes (Coquillett) (1905); Mexico

fuliginosa (Meigen) (1818); New Mexico, Arizona

occidentalis Wirth (1952); New Mexico

squamipes (Coquillett) (1902); Las Vegas, Texas, Oklahoma, New Mexico, South Dakota, Wyoming

texana texana (Long) (1902); Texas, Oklahoma

texana simulata Walley (1932); Idaho

wheeleri Long (1902); Texas

Alleghany

aurea Malloch (1915); Illinois

bipunctata (Linnaeus) (1767); Washington D.C., Illinois, District of Columbia, Maine, Pennsylvania, Maryland, Massachusetts, Michigan, Indiana, Wisconsin, Iowa, Missouri, Oklahoma, Louisiana, Texas.

brevipennis (Macquart) (1826); Pennsylvania, District of Columbia, Texas, Illinois, Michigan, Virginia, Maine, New York, New Jersey, Florida, Louisiana, Oklahoma, Missouri, Arkansas, Kansas, Indiana, North Dakota

cilipes (Coquillett) (1900); Illinois, District of Columbia

cinctipes (Coquillett) (1905); Florida

fuliginosa (Meigen) (1818); New Hampshire, Connecticut, Virginia, Tennessee, Georgia, Florida, New York, Mississippi, Louisiana, Washington

pergandei Coquillett (1901); Eastern United States

pilosa Coquillett (1902); Eastern United States

squamipes (Coquillett) (1902); Texas, Illinois, Louisiana, Kansas, Iowa, Washington

texana texana (Long) (1902); Missouri, Louisiana, District of Columbia, Oklahoma, Texas

townesi Wirth (1952); Washington

Canadian

bipunctata (Linnaeus) (1767); Ontario, British Columbia, Alaska

bipunctatapropinqua Chan (1965); Quebec

brevipennis (Macquart) (1826); Saskatchewan

cilipes (Coquillett) (1900); Alaska

fuliginosa (Meigen) (1818); Ontario, Manitoba

obscura Walker (1848); Canada

parva Walker (1848); Canada

texana simulata Walley (1932); Ontario

SUBGENUS WARMKEA SAUNDERS

ORIENTAL

Indo-Malayan

malayae Saunders (1956); Malaya

plus one species (Saunders, 1956)

NEOTROPICAL

Brazilian

bicolor Saunders (1956); Trinidad

spinosa Saunders (1956); British Guiana

terrestris Saunders (1956); Trinidad

tuberculata Saunders (1956); Trinidad, Tobago

Mexican

tuberculata Saunders (1956); Costa Rica

Antillean

aeria Saunders (1956); Puerto Rico

bicolor Saunders (1956); Puerto Rico

spinosa Saunders (1956); Puerto Rico, Dominica

plus one species close to aeria (Saunders, 1956)

NEARCTIC

Alleghany

one species close to aeria (Saunders, 1956)

GENUS ATRICHOPOGON KIEFFER

SUBGENUS ATRICHOPOGON KIEFFER

PALEARCTIC

European

alveolatus Nielsen (1951); Denmark

cornutus Nielsen (1951); Denmark

dubius Nielsen (1951); Denmark

fuscus (Meigen) (no date!); England

hexastichus Nielsen (1951); Denmark

infuscus Goetghebuer (1929); Belgium

minutus (Meigen) (1830); England

polydactylus Nielsen (1951); Denmark

speculiger Nielsen (1951); Denmark

Mediterranean

armaticrus Kieffer (1923); Biskra (Algeria)

biskraensis Kieffer (1923); Biskra (Algeria)

cataneii Kieffer (1923); Biskra (Algeria)

sahariensis Kieffer (1923); Biskra (Algeria)

transversalis Kieffer (1918); Asia Minor

ventralis Kieffer (1918); Asia Minor

trifasciatus Kieffer (1918); Asia Minor

Manchurian

akisukii Tokunaga (1940); Japan

boharti Tokunaga (1952); Ryukyu Is.

citrinipes Kieffer (1922); Ryukyu Is., Honshu

clavifuscus Tokunaga (1940); Japan

dorsalis Tokunaga (1940); Ryukyu Is., Honshu

ezoensis Tokunaga (1940); Japan

femoralis Tokunaga (1940); Japan

flavens Tokunaga (1940); Japan

flaviscutelum Tokunaga (1940); Japan

formosanus Kieffer (1918); Ryukyu Is.

insularis Kieffer (1921); Ryukyu Is.

jacobsoni (de Meijere) (1907); Ryukyu Is.

monticolus Tokunaga (1940); Japan

okinawensis Tokunaga (1962); Ryukyu Is.

palmatus Tokunaga (1962); Ryukyu Is., Honshu parviforceps Tokunaga (1940); Japan

pilosipennis Tokunaga (1940); Japan

ryukyuensis Tokunaga (1962); Ryukyu Is.

spiniventris Tokunaga (1940); Japan

unguis Tokunaga (1962); Ryukyu Is.

xanthopygus Tokunaga (1962); Ryukyu Is.

yoshimurai Tokunaga (1940); Kyoto

Ethiopian

celibatum Ingram and Macfie (1923); Mossel Bay, Cape Province

hirsutipennis Ingram and Macfie (1923); Mossel Bay, Cape Province

melanimum Ingram and Macfie (1923); Mossel Bay, Cape Province

natalensis Ingram and Macfie (1923); Natal

turneri Ingram and Macfie (1923); Mossel Bay, Cape Province

victoriae De Meillon (1942); S. Rhodesia

ORIENTAL

Ceylonese

horni Kieffer (1926); Ceylon

Indo-Chinese

argus Kieffer (1916); Taiwan

citrinipes Kieffer (1922); Taiwan

flaviceps var. mendax Kieffer (1922); Taiwan

formosanus Kieffer (1918); Taiwan

haemorrhoidalis Kieffer (1921); Taiwan

insularis Kieffer (1921); Taiwan

jacobsoni (de Meijere) (1907); Assam

kagiensis Tokunaga (1940); Taiwan

minimus Kieffer (1916); Taiwan

monticolus Tokunaga (1940); Taiwan

myrmedon Kieffer (1922); Taiwan

pruinosus Kieffer (1921); Taiwan

ruber Kieffer (1916); Taiwan

rufescens Kieffer (1921); Taiwan

Indo-Malayan

assuetus Macfie (1934); Malaya, Sumatra

attenta Johannsen (1932); Java

diluta Johannsen (1932); Java

discors Macfie (1934); Malaya

flavidus Kieffer (1921); Philippines

fulvus Macfie (1934); Malaya

jacobsoni (de Meijere) (1907); Malaya, Java, Philippines

nigripes Macfie (1934); Malaya

pudica Johannsen (1932); Java

subfuscus Macfie (1934); Malaya

subfuscus var. *melanotus* Macfie (1934); Malaya

sumatrae Macfie (1934); Sumatra, Malaya

AUSTRALIAN

Austro-Malayan

bifasciatus Kieffer (1917); New Guinea

biroi Kieffer (1917); New Guinea

immaculatus Kieffer (1917); New Guinea

jacobsoni (de Meijere) (1907); New Guinea, New Britain

sessilis Kieffer (1917); New Guinea

vestitipennis Kieffer (1917); New Guinea

Australian

atratus var. rufiventris Kieffer (1917); N.S. Wales

coracinus Kieffer (1917); N.S. Wales

Polynesian

arciforceps Tokunaga (1941); Micronesia

armaticaudalis Tokunaga and Murachi (1959); Micronesia

brevicornis Tokunaga (1959); Micronesia

fenestriscutum Tokunaga and Murachi (1959); Micronesia

flavenicruris Tokunaga and Murachi (1959); Micronesia

gressitti Tokunaga (1959); Micronesia

jacobsoni (de Meijere) (1907); Micronesia, Marquesas, Samoa, Tahiti, Fiji

raripilipennis Tokunaga and Murachi (1959); Micronesia

snyderi Tokunaga (1959); Micronesia

spinicaudalis Tokunaga (1959); Micronesia

New Zealand

fitzroyi Macfie (1932); N. Zealand (Nelson)

greyi Macfie (1932); N. Zealand (Otira)

hobsoni Macfie (1932); N. Zealand (Nihotapu, Weltons Bush, Waiho, Mt. Arthur)

? novae-zelandie Kieffer (1922); New Zealand

shortlandi Macfie (1932); N. Zealand (Aniseed Valley, Waiho, Lake Brunner, Kaitouna, Kaikoura, Maitai Valley, Mt. Arthur)

vestitipennis Kieffer (1917); N. Zealand (Mt. Arthur, Ohakune)

NEOTROPICAL

Chilean

albinensis Ingram and Macfie (1931); Patagonia, S. Chile

assimilis Ingram and Macfie (1931); Patagonia, S. Chile _chilensis_ Ingram and Macfie (1931); Patagonia, S. Chile

obfuscatus Ingram and Macfie (1931); Patagonia, S. Chile

obnubilus Ingram and Macfie (1931); Patagonia, S. Chile

Brazilian

adamsoni Macfie (1937); Trinidad

bifidus Ewen (1958); Nictheroy (Brazil)

caribbeanus Ewen (1958); Tobago

glaber Macfie (1936); Trinidad

gordoni Macfie (1938); British Guiana

guianensis Macfie (1940); British Guiana

harrisi Macfie (1938); Trinidad

nanus Macfie (1940); British Guiana

nebulosus Macfie (1939); Trinidad

remigatus Ewen (1958); Petropolis (Brazil)

tuberculatus Ewen (1958); Trinidad

umbratilis Macfie (1935); British Guiana

woodfordi Macfie (1938); British Guiana, Trinidad

Mexican

incultus Ewen (1958); Costa Rica

longicornis Ewen (1958); Costa Rica

Antillean

? _lituratus_ Williston (1896); St. Vincent Is.

obscurus Ewen (1958); Puerto Rico

saundersi Ewen (1958); Puerto Rico

? _sequax_ Williston (1896); St. Vincent Is.

? _thersites_ Williston (1896); St. Vincent Is.

NEARCTIC

Californian

arcticus (Coquillett) (1900); California

fusculus (Coquillett) (1901); California

levis (Coquillett) (1901); California

occidentalis Wirth (1952); California

transversus Wirth (1952); California

websteri (Coquillett) (1901); California

Rocky Mountain

articus (Coquillett) (1900); Colorado

fusculus (Coquillett) (1901); Wyoming, Montana, Nevada

levis (Coquillett) (1901); South Dakota, Texas, New Mexico, Utah

occidentalis Wirth (1952); Montana, New Mexico

websteri (Coquillett) (1901); Colorado

Alleghany

fusculus (Coquillett) (1901); New Jersey, District of Columbia, New Hampshire, Maine, Illinois, Maryland, Indiana, Louisiana, Massachusetts, Iowa

fusinervis Malloch (1915); Illinois

gilvus Coquillett (1905); Florida

levis (Coquillett) (1901); Maryland, Illinois, New York, New Jersey, Michigan, Massachusetts, Rhode Island, Connecticut, Ohio, District of Columbia, Indiana, Illinois, Louisiana, Texas

minutus (Meigen) (1830); Maryland, Indiana, Virginia

peregrinus Johannsen (1908); New York

Canadian

arcticus (Coquillett) (1900); Alaska, British Columbia

crinitus Ewen (1958); Nanaimo, Saskatchewan corpulentus Ewen (1958); Nanaimo

flavus Ewen (1958); Saskatoon

fusculus (Coquillett) (1901); Ontario

humicolus Ewen (1958); Nanaimo

inconspicuus Ewen (1958); Saskatoon

maculosus Ewen (1958); Saskatoon

minutus (Meigen) (1830); Truro, Nanaimp

occidentalis Wirth (1952); Alaska

polydactylus Nielsen (1951); Saskatoon

SUBGENUS MELOEHELEA WIRTH

PALEARCTIC

European

meloesugans Kieffer (1922); England, Finland

oedemerarum Störa (1939); England, Finland, Denmark
Germany, Sweden

rostratus Winnertz (1852); Denmark

Mediterranean

meloesugans Kieffer (1922); Algeria

ETHIOPIAN

West African

meloesugans Kieffer (1922); Algeria

NEARCTIC

Californian

epicautae Wirth (1956); California

Rocky Mountain

epicautae Wirth (1956); Arizona

Alleghany

farri Wirth (1956); Massachusetts

oedemerarum Stora (1939); Virginia, Maryland, New Hampshire

Canadian

epicautae Wirth (1956); British Columbia

GENUS LASIOHELEA KIEFFER

SUBGENUS LASIOHELEA S. STR. KIEFFER

PALEARCTIC

European

pilosipennis Kieffer (1919); Hungary

velox (Winnertz) as pilosipennis Kieffer (1919); Europe

Manchurian

longicornis (Tokunaga) (1940); Honshu, Ryukyu Is.

? minima Tokunaga (1940); Japan

? minuta Tokunaga (1940); Japan

? nipponica Tokunaga (1940); Japan

ETHIOPIAN

East African

? lefanni var. squamipes Ingram and Macfie (1924); Zanzibar

West African

atratula (Goetghebuer) (1935); Belgian Congo

? brevicosta Clastrier (1960); Congo

? brevitarsata Ingram and Macfie (1924); Gold Coast

? caliginosa Ingram and Macfie (1924); Gold Coast

? dewulfi Goetghebuer (1933); Belgian Congo

? inconspicuosa Ingram and Macfie (1924); Gold Coast

? litoraurea Ingram and Macfie (1924); Gold Coast

? maculipes Goetghebuer (1933); Belgian Congo

ORIENTAL

Indo-Malayan

flavescens (Saunders) (1964); Philippines

longineura (Saunders) (1964); Philippines

propria Chan (1965); Singapore

? stimulans (de Meijere) (1909); Sumatra, Java

uncuspromissa Chan (1965); Singapore

AUSTRALIAN

Australian

townsvillensis (Taylor) (1914); Queensland

Polynesian

? ancoriformis (Tokunaga) (1959); Micronesia

carolinensis (Tokunaga) (1940); Micronesia

spinipes (Tokunaga) (1959); Micronesia

? stimulans (de Meijere) (1909); Micronesia

NEOTROPICAL

Chilean

? shannoni Ingram and Macfie (1931); Correntoso (Chile)

Brazilian

attenuata (Saunders) (1964); Trinidad

cornuta (Saunders) (1964); Trinidad, Santos (Brazil)

? danaisi Floch and Abonnenc (1949); Venezuela

? louriei Macfie (1935); Tutoia, Pianhi

Mexican

attenuata (Saunders) (1964); Costa Rica

cornuta (Saunders) (1964); Costa Rica

? _fluviatilis_ (Lutz) (1914); Rio Negro, Massaraby

intermedia (Saunders) (1964); Costa Rica

quasicornuta (Saunders) (1964); Costa Rica

NEARCTIC

Alleghany

fairfaxensis Wirth (1951); Virginia, Massachusetts, Michigan

Canadian

? _cretea_ Boesel (1937); Canad

fairfaxensis Wirth (1951); Ontario

? _globosa_ Boesel (1937); Canada

NEW SUBGENUS (LANE'S _LASIOHELEA_ _STYLIFER_ LUTZ)

NEOTROPICAL

Brazilian

stylifer (Lutz) (1913); British Guiana, Rio de Janeiro, Trinidad

Mexican

stylifer (Lutz) (1913); Panama

SUBGENUS _DACNOFORCIPOMYIA_ CHAN AND SAUNDERS

ORIENTAL

Indo-Malayan

? _agas_ as _ceratopogon_ _agas_ Rondani (1875); Borneo

anabaenae (Chan and Saunders) (1965); Singapore

SUBGENUS *THYRIDOMYIA* SAUNDERS

PALEARCTIC

European

frutetorum (Winnertz) (1852); Europe

palustris (Saunders) (1925); England

Manchurian

kitasirakawae (Tokunaga) (1940); Japan

ETHIOPIAN

West African

aethiopiae (Ingram and Macfie) (1924); Gold Coast

skiaphila Clastrier (1960); Congo

ORIENTAL

Indo-Malayan

gossympina Chan (1965); Singapore

vertexcava Chan (1965); Singapore

AUSTRALIAN

Polynesian

esakii Tokunaga (1940); Micronesia

hamata (Tokunaga) (1959); Micronesia

NEOTROPICAL

Brazilian

nana Macfie (1944); Brazil, Trinidad

Mexican

nodosa (Saunders) (1959); Costa Rica

NEARCTIC

Californian

monilicornis (Coquillett) (1905); California

Alleghany

monilicornis (Coquillett) (1905); Maryland, Indiana

Canadian

aspinosa (Saunders) (1956); Saskatoon

monilicornis (Coquillett) (1905); British Columbia, Quebec, Alaska

palustris (Saunders) (1925); Nanaimo

sp. A (Saunders, 1956); Saskatoon

SUBGENUS *SYNTHYRIDOMYIA* SAUNDERS

PALEARCTIC

Europe

knockensis (Goetghebuer) (1938); Belgium

murinus (Winnertz) (1852); England

Mediterranean

moascari (Macfie) (1943); Moascar (Egypt)

Manchurian

acidicola Tokunaga (1937); Honshu

Kii Tokunaga (1940); Japan

longitarsus Tokunaga (1940); Japan

ETHIOPIAN

East African

corsoni (Macfie) (1926); Dar-Es-Salaam

AUSTRALIAN

Polynesian

unituberculata (Tokunaga) (1959); Micronesia

NEOTROPICAL

Chilean

sanctaeclarae (Wirth) (1952); Juan Fernandez

Brazilian

tenuiforceps (Macfie) (1939); Brazil

NEARCTIC

Californian

colemani (Wirth) (1952); California

Canadian

sp. A (Saunders, 1956); Saskatoon

GENUS *NEOFORCIPOMYIA* TOKUNAGA

PALEARCTIC

European

eques (Johannsen) (1908); Finland, Britain, Austria, Sweden Norway, Germany

papillionivora (Edwards) (1923); England

Manchurian

eques (Johannsen) (1908); Hokkaido

okadai (Tokunaga) (1939); Japan

ETHIOPIAN

East African

insignicornis (Macfie) (1947); Uganda

ORIENTAL

Indo-Malayan

equitans (Edwards) (1933); North Borneo

pectiunguis (de Meijere) (1923); Sumatra

AUSTRALIAN

Austro-Malayan

pennambula (Macfie) (1932); Moluccas

tipulivora (Macfie) (1936); New Guinea

Australian

four species (Saunders, 1964)

Polynesian

basiflava (Tokunaga) (1959); Micronesia

pectiunguis (de Meijere) (1923); Micronesia, Samoa

samoensis (Edwards) (1928); Samoa

NEOTROPICAL

Chilian

intrepida (Macfie) (1936); Peru

Brazilian

aeronautica (Macfie) (1935); British Guiana

? opilionivora (Lane) (1947); Sao Paulo (Brazil)

trinidadensis (Saunders) (1964); Trinidad

Mexican

mexicana (Wirth) (1956); Mexico

NEARCTIC

Rocky Mountain

baueri (Wirth) (1956); Arizona

Alleghany

eques (Johannsen) (1908); Michigan, New York

mcateei (Wirth) (1956); Maryland

Canadian

crinita (Saunders) (1964); Saskatoon

eques (Johannsen) (1908); Quebec, British Columbia, Nanaimo

saundersi Chan (1965); Quebec

sp. A (Saunders, 1964); Saskatoon

sp. B (Saunders, 1964); Saskatoon

GENUS TRICHOHELEA GOETGHEBUER

PALEARCTIC

Manchurian

tsutsumii (Tokunaga) (1960); Japan

sp. inc. J. No. 1 (Tokunaga, 1960); Kyoto

ORIENTAL

Indo-Malayan

comis (Johannsen) (1932); Sumatra, Java

grandis Chan (1965); Singapore

nicopina Chan (1965); Singapore

AUSTRALIAN

Austro-Malayan

comis (Johannsen) (1932); Bali

New Zealand

austrina (Macfie) (1932); Reefton, Aniseed Valley

Polynesiah

brevis (Johannsen) (1927); Hawaii

hamaticauda (Tokunaga) (1959); Micronesia

oligarthra (Saunders) (1956); Micronesia

sabroskyi (Tokunaga) (1959); Micronesia

NEOTROPICAL

Brazilian

caribbeana (Saunders) (1956); Trinidad, British Guiana, Tobago

oligarthra (Saunders) (1956); British Guiana

Mexican

oligarthra (Saunders) (1956); Mexico

Antillean

<u>antiguensis</u> (Saunders) (1956); Antigua

<u>jocosa</u> (Saunders) (1956); Trinidad

<u>oligarthra</u> (Saunders) (1956); Puerto Rico, Cuba, Dominca, Montserrat

GENUS <u>PTEROBOSCA</u> MACFIE

PALEARCTIC

European

<u>Pterobosca</u> <u>paludis</u> Macfie (1936); England, France

Manchurian

<u>Pterobosca</u> <u>adhesipes</u> Macfie (1932); Ryukyu Is.

<u>Forcipomyia</u> <u>(Pterobosca)</u> <u>asahinai</u> Tokunaga (1962); Ryukyu Is.

<u>Pterobosca</u> <u>fidens</u> Macfie (1936); Ryukyu Is.

<u>Pterobosca</u> <u>latipes</u> Macfie (1936); Ryukyu Is.

<u>Pterobosca</u> <u>tokunagai</u> Oka and Asahina (1948); Ryukyu Is., Honshu

ETHIOPIAN

West African

<u>Pterobosca</u> <u>mollipes</u> Macfie (1932); Liberia, Senegal

East African

<u>Pterobosca</u> <u>mollipes</u> Macfie (1932); Senegal

<u>Pterobosca</u> <u>paludis</u> Macfie (1936); Uganda

ORIENTAL

Indo-Chinese

<u>Pterobosca</u> <u>aerobates</u> Macfie (1936); Assam

<u>Certaopogon</u> <u>aeschnosuga</u> de Meijere (1923); Taiwan

<u>Pterobosca</u> <u>fidens</u> Macfie (1936); Hainan, Taiwan, China

<u>Pterobosca</u> <u>latipes</u> Macfie (1936); Hainan, China

Indo-Malayan

<u>Pterobosca adhesipes</u> Macfie (1932); Java Sea

<u>Ceratopogon aeschnosuga</u> de Meijere (1923); Sumatra, Java

AUSTRALIAN

Austro-Malayan

<u>Pterobosca adhesipes</u> Macfie (1932); New Guinea

<u>Pterobosca ariol</u> Macfie (1932); Moluccas

<u>Pterobosca lairdi</u> Wirth (1956); Solomon Is.

<u>Pterobosca odonatiphila</u> Macfie (1932); New Guinea

Polynesian

<u>Pterobosca adhesipes</u> Macfie (1932); Ponape and Kusaie (Micronesia)

<u>Forcipomyia (Pterobosca) chrysopae</u> Tokunaga (1959); Micronesia

<u>Pterobosca esakii</u> Tokunaga (1940); Micronesia

<u>Pterobosca feminae</u> Tokunaga (1940); Micronesia

<u>Pterobosca fidens</u> Macfie (1936); Micronesia

NEOTROPICAL

Brazilian

<u>Ceratopogon fusicornis</u> Coquillett (1905); Brazil, Columbia

Mexican

<u>Pterobosca incubans</u> Macfie (1937); British Honduras, Mexico

Antillean

<u>Ceratopogon fusicornis</u> Coquillett (1905); Puerto Rico

<u>Pterobosca incubans</u> Macfie (1937); Puerto Rico

NEARCTIC

Alleghany

<u>Ceratopogon fusicornis</u> Coquillett (1905); Florida, Louisiana

GENUS PARAPTEROBOSCA HARANT & HUTTEL

ETHIOPIAN

West African

Parapterobosca anthropophila Harant & Huttel (1951);
Ivory Coast

Most genera and subgenera of the Forcipomyiinae have world wide distribution (Table 1), especially Forcipomyia s. str., Proforcipomyia, Lasiohelea s. str., Thyridomyia, Neoforcipomyia and Pterobosca. The absence or paucity of midges in the Mediterranean, Siberian, South African, Malagasy, Indian, Ceylonese and New Zealand subregions, is probably not indicative of the true nature of distribution of these forms but indicative of the lack of attention given to this subfamily by entomologists of these regions. It appears that where collections of either the immature stages or the imagines or both are carried out intensively and extensively, most of the known genera and subgenera of the Forcipomyiinae are found. It would not be surprising in time to find that most, if not all, genera and subgenera are of universal occurrence. This possibility is strengthened when one considers the conditions that favour and limit the dispersal of these forms.

CONDITIONS LIMITING DISPERSAL

(a) Food.- The larvae of Forcipomyiinae have a wide range of habitats - rotting wood and bark, hollow roots and stems of dead plants, cacti, horse and cow dung, tree holes, sap of tree wounds, watery detritus in leaf axils of plants, mosses and algae on wood, rocks or soil, etc. -

TABLE 1. WORLD DISTRIBUTION OF THE FORCIPOMYIINAE

ZOOGEOGRAPHICAL REGIONS — REGIONS	PALEARCTIC				ETHIOPIAN				ORIENTAL				AUSTRALIAN				NEOTROPICAL				NEARCTIC			
GENUS (Subgenus) — SUB-REGIONS	European	Mediterranean	Siberian	Manchurian	East African	West African	South African	Malagasy	Indian	Ceylonese	Indo-Chinese	Indo-Malayan	Austro-Malayan	Australian	Polynesian	New Zealand	Chilian	Brazilian	Mexican	Antillean	Californian	Rocky Mountain	Alleghany	Canadian
Forcipomyia (*Forcipomyia*)	x	x		x	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
(*Schizoforcipomyia*)		x?									x?	x			x?									x
(*Warmkea*)												x						x	x	x			x	
Metaforcipomyia																		x						
Proforcipomyia	x			x		x					x	x	x		x			x	x	x	x	x	x	
Caloforcipomyia				x		x?					x		x		x			x					x?	
Lasiohelea (*Lasiohelea*)	x			x	x	x						x	x	x	x		x?	x	x				x	x
(L. *stylifer* Lutz)																		x	x					
(*Dacnoforcipomyia*)												x												
(*Thyridomyia*)	x			x		x						x			x			x	x		x		x	x
(*Synthyridomyia*)	x	x		x	x										x		x	x			x			x

TABLE 1. WORLD DISTRIBUTION OF THE FORCIPOMYIINAE

ZOOGEOGRAPHICAL REGIONS — REGIONS	PALEARCTIC				ETHIOPIAN				ORIENTAL				AUSTRALIAN				NEOTROPICAL				NEARCTIC			
GENUS (Subgenus) — SUB-REGIONS	European	Mediterranean	Siberian	Manchurian	East African	West African	South African	Malagasy	Indian	Ceylonese	Indo-Chinese	Indo-Malayan	Austro-Malayan	Australian	Polynesian	New Zealand	Chilian	Brazilian	Mexican	Antillean	Californian	Rocky Mountain	Alleghany	Canadian
Atrichopogon																								
(Atrichopogon)	x	x		x			x			x	x	x	x		x	x	x	x	x	x	x	x	x	x
(Meloehelea)	x	x				x															x	x	x	x
Trichohelea				x								x	x		x			x	x	x				
Neoforcipomyia	x			x	x							x	x	x	x		x	x	x			x	x	x
Pterobosca	x			x	x	x					x	x	x		x			x	x	x			x	
Parapterobosca						x																		
No. of genera and subgenera represented	(8);(6-1?)				(7-1?);(4)				(8); (7)				(8);(5-1?)				(9); (7)				(6-1?);(7)			
Times each region represented	23 - 1(?)				12 - 2(?)				19 - 1(?)				23 - 1(?)				33 - 1(?)				28 - 1(?)			
													42 - 2(?)											

x denotes presence

all of which are universally found. Larvae are not restricted therefore except where food specificity is extreme and in these cases distribution would follow the distribution of the host plants.

The adults of Forcipomyiinae also have a wide range of feeding habits, ranging from feeding on nectar of plants to sucking of blood from insects, arachnids, amphibians, reptiles and mammals. Since these food sources for adults are universally obtainable, the distribution of the Forcipomyiinae would accordingly be universal save in the case of species that are host specific.

(b) *Temperature.* Temperature which would be expected to have an important influence on the geographical distribution of midges does not appear to be of very great importance as *Forcipomyia fuliginosa* and possibly many other species occur over a wide range of countries (see Table 2).

(c) *Other Environmental Factors*. Physical barriers of the environment, such as deserts, mountains and vast expanse of sea, appear to be relatively unimportant in limiting the range of midges since they can be carried by strong winds and air currents, over great distances. In fact, Gislen (1948) considers that these minute insects are so easily carried by air currents that they are not subject to the same distributional limitations as other insects and are therefore of no significance in zoogeography. This contention has however been disputed and challenged by many zoogeographers (Gressitt, 1958).

CONDITIONS FAVOURING DISPERSAL

(a) *Flight.* In general, insects, like birds, owe their wide distribution to their great powers of flight. In the ceratopogonids, where the power of flight is limited (Kettle, 1951), transport over long distances is accomplished by air currents.

(b) *Transporting Vehicles.* Many species undoubtedly lay their eggs on decaying and rotting timbers of ships and other ocean vessels and can be carried over vast distances. Floating logs of decaying wood in rivers, streams and oceans (debris rafts; Matthew, 1915) aid in the dispersal of early stages. Biting species can also be transported over long distances on the bodies of animals, including man.

The distribution of the Forcipomyiinae, although at present only poorly understood, indicates that the Neotropical Region (if the Oriental is not combined with the Australian) contains by far the richest fauna of this subfamily, with nine out of the ten genera and seven out of the ten subgenera represented. The genus *Metaforcipomyia* and the subgenus (Lane's *Lasiohelea stylifer* Lutz) are peculiar to the region and are likely endemic forms of it. Of this region, the Brazilian subregion has the richest fauna with *Warmkea*, *Lasiohelea* s. str., *Neoforcipomyia*, *Proforcipomyia* and *Atrichopogon* species in particular being well represented here. This is to be expected since midge fauna is closely associated with plant flora and the Brazilian subregion, being essentially tropical, has an unusually luxuriant flora.

Ranking next to the Neotropical, in number of genera and subgenera, is the Oriental Region which is poorly represented in numbers of species particularly in the Indian and Ceylonese subregions where Forcipomyiinae are hardly known. In other Oriental subregions Forcipomyiinae midges have not been well collected and it is almost certain that in time many additional species will be discovered. From the known species distribution the fauna in the Indo-Malayan subregion is the richest, with one subgenus, *Dacnoforcipomyia*, peculiar and likely endemic to it. The region is particularly rich in *Lasiohelea* s. str., and shares the highest number of known species with the Mexican subregion of the Neotropical.

TABLE 2. DISTRIBUTION OF THE BETTER KNOWN SPECIES OF THE FORCIPOMYIINAE

ZOOGEOGRAPHICAL REGIONS / REGIONS	NEOTROPICAL				NEARCTIC				PALEARCTIC				ORIENTAL				AUSTRALIAN				ETHIOPIAN			
SUB-REGIONS / GENUS (Subgenus) species	Chilian	Brazilian	Mexican	Antillean	Californian	Rocky Mountain	Alleghany	Canadian	European	Mediterranean	Siberian	Manchurian	Indo-Chinese	Indo-Malayan	Ceylonese	Indian	Austro-Malayan	Polynesian	New Zealand	Australian	East African	West African	South African	Malagasy
PROFORCIPOMYIA																								
formosana												x	x											
ingrami				x										x				x				x		
sauteri												x	x				x	x						
yapensis												x						x						
CALOFORCIPOMYIA																								
takahashii												x	x											
FORCIPOMYIA																								
(Schizoforcipomyia)																								
?fuscimanus												x	x					x						
(Forcipomyia s. str.)																								
bipunctata					x	x	x	x	x			x												
brevipennis					x	x	x	x	x			x												
edgari												x						x						
esakiana												x	x				x	x						
formosae												x	x											
fuliginosa	x	x	x	x	x	x	x	x	x			x	x	x	x		x	x		x	x	x		
raleighi		x							x															
(Warmkea)																								
?aeria				x			x																	

TABLE 2. DISTRIBUTION OF THE BETTER KNOWN SPECIES OF THE FORCIPOMYIINAE

ZOOGEO-GRAPHICAL REGIONS — REG-IONS	NEOTROPICAL				NEARCTIC				PALEARCTIC				ORIENTAL				AUSTRALIAN				ETHIOPIAN			
GENUS (Subgenus) species — SUB-REG-IONS	Chilian	Brazilian	Mexican	Antillean	Californian	Rocky Mountain	Alleghany	Canadian	European	Mediterranean	Siberian	Manchurian	Indo-Chinese	Indo-Malayan	Ceylonese	Indian	Austro-Malayan	Polynesian	New Zealand	Australian	East African	West African	South African	Malagasy
ATRICHOPOGON																								
(*Atrichopogon*)																								
formosanus												x	x											
jacobsoni												x	x	x			x	x						
minimus												x	x											
minutus							x	x	x															
polydactylus								x	x															
(*Meloehelea*)																								
meloesugans									x	x												x		
oedemerarum							x		x															
LASIOHELEA																								
(*Lasiohelea* s. str.)																								
?*stimulans*														x				x						
(*Thyridomyia*)																								
palustris								x	x															
NEOFORCIPOMYIA																								
eques							x	x	x			x												
pectiunguis														x				x						

TABLE 2. DISTRIBUTION OF THE BETTER KNOWN SPECIES OF THE FORCIPOMYIINAE

ZOOGEOGRAPHICAL REGIONS REGIONS	NEOTROPICAL				NEARCTIC				PALEARCTIC				ORIENTAL				AUSTRALIAN				ETHIOPIAN			
GENUS (Subgenus) species SUB-REGIONS	Chilian	Brazilian	Mexican	Antillean	Californian	Rocky Mountain	Alleghany	Canadian	European	Mediterranean	Siberian	Manchurian	Indo-Chinese	Indo-Malayan	Ceylonese	Indian	Austro-Malayan	Polynesian	New Zealand	Australian	East African	West African	South African	Malagasy
TRICHOHELEA																								
comis														x			x							
oligarthra		x	x	x														x						
PTEROBOSCA																								
adhesipes												x		x			x	x						
fidens												x	x					x						
fusicornis		x		x			x																	
latipes												x	x											
paludis									x												x			

x denotes presence

From Table 2 which shows the distribution of the better known Forcipomyiinae species, we find that many of the Oriental species are common in both the Australian and Palearctic regions, the last two ranking third in the number of world genera represented. The species common to both the Oriental and Palearctic regions belong mainly to the Indo-Chinese (mainly Taiwan) and Manchurian (mainly Japan) subregions, respectively. Those common to the Oriental and Australian regions belong, respectively, to the Indo-Chinese and Indo-Malayan subregions and to the Austro-Malayan and Polynesian subregions. Also, the distribution of the better known species of the Forcipomyiinae demonstrates that the fauna between the Palearctic and Nearctic and also Palearctic (mainly European) and Ethiopian, is distinct while that between the New World (North, Central and South Americas) and the Old World, except Palearctic is indistinct. On the basis of the above evidence, it would appear that the Forcipomyiinae originated and evolved in the Oriental Region, with the original centre of radiation being the Malay Archipelago (Sundaland). This possibility is most likely since historically and geologically the Malay Archipelago forms a connecting link between the Indo-Chinese and Austro-Malayan subregions, the islands comprising Sundaland being situated on the Asiatic Continental Shelf and forming a compact land mass during the Pleistocene (Gupta, 1962). This is in agreement with Khalaf's (1954) findings for Culicoides which, according to him, evolved in and spread out from, the Oriental Region or from farther north when the climate was warmer. All the above information seems to support the Wegenerian Hypothesis or theory of continental drift.

The genera and subgenera with the widest distribution, namely Atrichopogon, Forcipomyia s. str., Proforcipomyia, Lasiohelea s. str.

Thyridomyia, *Neoforcipomyia* and *Pterobosca*, are presumably the most ancient, assuming they originally had a common centre of radiation in the Oriental Region. Lane's *Lasiohelea stylifer* Lutz, *Dacnoforcipomyia anabaenae* and *Parapterobosca anthropophila*, all man-biting forms, on the other hand, must be fairly recent forms since they are restricted in their distribution and are most likely endemic forms of the Neotropical, Oriental and Ethiopian regions, respectively. This would suggest that the man-biting habit has a very recent origin. Since in the Forcipomyiinae the insect-biting forms (most *Neoforcipomyia*, *Pterobosca* and some *Forcipomyia* s. str. species) outnumber the vertebrate biting forms (some *Lasiohelea* s. str. species, *Dacnoforcipomyia anabaenae*, and two *Atrichopogon* species?) and the former has wider distribution than the latter, it follows that insect-biting is more primitive than vertebrate-biting, a problem which Downes (1958) has already drawn attention to as difficult to determine.

Although the Palearctic Region shares many identical species with the Oriental only the Manchurian Subregion (chiefly Ryukyu Islands) really shows homogeneous fauna (not only the Forcipomyiinae but most insects) with the Indo-Chinese (chiefly Taiwan) of the Oriental. For this reason Gressitt (1961) considers the Ryukyu Islands as belonging to the Oriental Region rather than to Wallace's Palearctic Region. From zoogeographical studies of Pacific and Antarctic insects, Gressitt (loc.cit.) was also able to demonstrate that Wallace's assignment of the islands eastward of Borneo (east of Wallace's Line) to the Australian Region, is not valid for insects although valid for vertebrates. Wallace's Australian Region includes Australia, Tasmania, the islands on the Sahul Shelf, Melanesia including New Guinea, Hawaii and the South Pacific Islands including Micronesia, Samoa and Southeast Polynesia but Gressitt (1956, 1958, 1961), from faunal studies and floral considerations, considers only Australia, Tasmania, New Zealand, the Chatham Islands and the Southern part of New Guinea, as belonging to the Australian Region, the rest as belonging to the Oriental.

Gressitt (1961) found that the insect fauna of the entire Pacific oceanic area and of the islands of the Southwest Pacific belongs to the Oriental Region. The Oriental Region of Gressitt would then include Wallace's traditional subregions plus the islands from Lord Howe Island, Norfolk Island, Kermadec Islands, Rapa and Ester, northward to Hawaii, westward to the Bonins and Palau and again eastward and southward to include the New Hebrides, Santa Cruz Islands and New Caledonia. The other islands, "subcontinental" and continental, westward of this great oceanic area, from the Solomon Islands westward to S.E. Asia, and as far north as the Ryukyu Islands also belong here.

In the Australian Region, New Zealand's fauna is very different from that of Australia (Gressitt, 1961) (also shown by the Forcipomyiinae) but New Caledonia possesses special forms common to both Australia and New Zealand and also to New Guinea. The Australian Region is bridged with the Oriental Region in faunal characteristics by the area between them. According to Gupta (1962), this intermediate area situated between the Australian and Asiatic continental shelves, comprising of Celebes, the Moluccas, New Guinea, the Bismarks, Solomons and nearby islands (or what has been called the Papuan Subregion of the Oriental by Gressitt) does not belong zoogeographically to either the Australian or Oriental regions but forms a region of its own, its main features being that of faunistic transition. Agreement differs as to which of these islands should be associated with the Oriental and which to the Australian Region. Mayr (1944) and Gressitt (1956) include them in the Oriental, but Wallace (1876) included them in the Australian Region.

The distribution of the Forcipomyiinae supports Gressitt's (1961) findings that New Guinea's insect fauna is primarily Oriental. This shows that New Guinea apparently had early relationships with Asia through fluctuating bridges or series of "stepping stones". It was apparently greatly isolated from Australia during much of the Tertiary and each of the two land masses developed its own characteristic fauna. It however has much affinity with Australia in the bird, reptile and mammal faunas.

The question of the origin and history of the Forcipomyiinae will undoubtedly be better understood when their zoogeographical distribution is greatly improved through extensive and intensive collections.

VIII. PHYLOGENY OF THE FORCIPOMYIINAE

A. INTRODUCTION

According to Hennig (1965), the method of phylogenetic systematics has the following basis: "that morphological resemblance between species cannot be considered simply as a criterion of phylogenetic relationship but that this concept should be divided into the concepts of symplesiomorphy, convergence and synapomorphy, but that only the last-named category of resemblance can be used to establish states of relationship." Thus, a polyphyletic group is formed, when in that group, species agreement rests on convergence; a paraphyletic group is formed when in that group, species agreement rests on symplesiomorphy, and a monophyletic group is formed when member species in that group can be considered to be more closely related to one another than to species outside these groups (Hennig, 1953), i.e. when species agreement rests on synapomorphy.

The degree of phylogenetic relationship that exists between species and groups has often been measured solely by the degree of morphological resemblance. This approach is obviously erroneous since it is concerned with resemblance or difference between organisms rather than with relationship between convergent or divergent characters and earlier conditions (Hennig, lo. cit.). Animal populations being communities of reproduction are not morphologically but genetically defined and measurement of the degree of phylogenetic relationship, rightly interpreted, is recency of common ancestry (Bigelow, 1956).

The phylogeny of the Ceratopogonidae has not so far been critically examined by systematists of these insects. The present study is an attempt to discover appropriate degrees of phylogenetic relationship that exist particularly between species or species groups in the Forcipomyiinae.

B. CONSIDERATIONS ON THE CERATOPOGONIDAE

First, let us consider the systematic position of the Ceratopogonidae and of the groups within this family.

The Ceratopogonidae has been classified by Hennig (1950) in the super-family Tendipedidea which includes the families Thaumaleidae, Tendipedidae (Chironomidae) and Simuliidae. According to Hennig (1950), and generally unanimous among most dipterists, the Ceratopogonidae are closest to the Chironomidae in which they were once a subfamily, and the Thaumaleidae. Downes (1950) from a study of the feeding habits of biting flies, concludes that the Ceratopogonidae, together with other biting nematocerans, as a group, are the closest existing representatives of the original Diptera which order is the most highly specialized of the panorpoid orders (Hinton, 1958).

Different ceratopogonid systematists have classified the family into various groups or subfamilies, some based on one or two arbitrary criteria, others on several. Edwards (1926) subdivided it into two groups on feeding habits: (i) forms whose females have blood-sucking habits, including *Culicoides*, *Forcipomyia* and *Atrichopogon*, and (ii) forms whose females prey on other smaller insects, including *Palpomyia*, *Bezzia* and *Stilobezzia*. Kieffer (1925) based his classification mainly on morphological forms and divided it into five groups on adult forms: *Forcipomyia*, *Dasyhelea*, *Culicoides*, *Palpomyia* and *Bezzia*; and three groups on larval forms: a genuine group including *Forcipomyia* and *Atrichopogon*; an intermediate group including Dasyhelea; and a vermiform group including Culicoides, Stilobezzia, Bezzia and Palpomyia. Mayer (1934) subdivided the family into six groups: Forcipomyia, Dasyhelea, Culicoides, Stilobezzia, Palpomyia and Leptoconops chiefly on structure of larval mouthparts. Enderlein (1936) recognized five subfamilies: Leptoconopinae, Forcipomyiinae, Ceratopogoninae, Palpomyiinae and Bezziinae. Macfie (1940) generally followed Mayer (1934) and Enderlein (1936) but considered that apart from Leptoconopinae, all the other subfamilies are untenable because of the common occurrence of annectant forms between them. He proposed nine groups: (i) Leptoconops group, (ii) Forcipomyia group, (iii) Dasyhelea group, (iv) Culicoides group, (v) Ceratopogon group, (vi) Stilobezzia group, (vii) Macropeza group, (viii) Palpomyia group and (ix) Bezzia group. Johannsen (1943) has also subdivided the family in a very similar way to Macfie but divides Macfie's Forcipomyia group into two groups -- Forcipomyia and Atrichopogon groups -- and combines two of Macfie's groups into one (Palpomyia and Bezzia groups).

Lee (1948) accepted Johannsen's division of Macfie's Forcipomyia group into Forcipomyia and Atrichopogon groups but retained Macfie's other groups so that in all he had ten groups. He divided the family into three major divisions: the first comprising of the Leptoconops group, the second of the Forcipomyia, Atrichopogon, Dasyhelea, Culicoides and Ceratopogon groups, and the third of the Stilobezzia, Macropeza, Palpomyia and Bezzia groups. Lee (lo. cit.) considered that the Leptoconops group alone is discontinuous from the rest of the family and thus deserves subfamily status. His three major divisions are morphologically fairly distinct and appear to coincide with the adult feeding habits: the first division comprises forms whose adult females suck blood from birds and mammals; the second division, a heterogeneous group, consists of forms (except Dasyheleinae) whose females suck blood from a wide range of hosts --- insects, arachnids, amphibians, reptiles, birds, and mammals -- and the last division comprises forms whose females prey on other smaller insects.

Wirth (1952) subdivided the Ceratopogonidae into four subfamilies: Leptoconopinae, Dasyheleinae, Forcipomyiinae and Heleinae, the last subfamily including Mayer's (1934) three groups: Culicoides, Stilobezzia and Palpomyia taken together with Helea. Tokunaga and Murachi (1959) considered Wirth's system most acceptable as a natural one but felt that his "Heleinae" requires closer discussion showing the more intimate evolutional relationship between adults and immature forms. They therefore refrained from classifying the family into subfamilies.

Systematists of the Ceratopogonidae have never experienced difficulty in distinguishing the Forcipomyiinae, obviously a monophyletic group, from other subfamilies. The adults are distinguished from other subfamilies by having well-developed empodia except in some males of Trichohelea where they are absent or vestigial, and the larvae are distinguished from other ceratopogonids according to Thomsen (1937), Hennig (1950) and Hardy (1960) by having prothoracic prolegs and short spines on all body segments. Another character which separates this subfamily from the rest of the family is the retention, in most species, of the last larval skin in the last few abdominal segments.

The Dasyheleinae, like the Forcipomyiinae, is also a monophyletic group and is easily separated from other groups by larval morphology and adult male genitalic characters. Among all the ceratopogonid groups it is the closest to Forcipomyiinae. Difficulty in distinguishing adult females of Dasyhelea and Lasiohelea species has often arisen from their close morphological similarity, especially in wing and antennal characters (Lee and Reye, 1954). The larvae of the two groups also show closest affinity with each other in the family in their common possession of well-developed mouthparts with pharynges possessing six combs. The two groups therefore are paraphyletic groups with respect to each other since their resemblance rests on symplesiomorphy.

The Leptoconopinae as a group is also monophyletic but its phyletic relationship with the other groups of the family is uncertain. Downes (1958) believes, from the feeding habits of adults and morphology of their mouthparts,that Leptoconops is closer to Culicoides than generally held. Both these groups attack birds and mammals in their female adult stage. Wirth (1952) and his followers, however, believe that the Culicoides group is closer to the other groups of the Ceratopogoninae than to the Leptoconopinae from larval and imaginal morphology. This view is currently held by most systematists of the Ceratopogonidae, and it therefore considers the Ceratopogoninae as a monophyletic group. The splitting of the Ceratopogoninae by Lee (1948) into two major groups, the Culicoides and Ceratopogon groups on the one hand and Stilobezzia, Macropeza, Palpomyia and Bezzia groups on the other, is supported by Downes' (1958) findings. Whether the Ceratopogoninae, in Lee's and Downes' sense, as a group, is monophyletic or polyphyletic, is therefore uncertain. Whether Wirth's (1952) Leptoconopinae and Ceratopogoninae are closer to each other and as a group or separately are closer to the Forcipomyiinae on the one hand, and Dasyheleinae on the other, is a problem to be solved in the future. The important task in the future would be to discover which characters in these various groups are apomorphic, which are plesiomorphic and which convergent. Present evidence from male genitalic characters appears to support the view that in the Ceratopogoninae the Culicoides and Ceratopogon groups, which are most closely related to each other (Lee, 1948), are as a group closer to the Forcipomyiinae and Dasyheleinae than is the Leptoconopinae to these latter groups. The remaining groups of the Ceratopogoninae are closer to the Culicoides and Ceratopogon groups, and as a group, are closer than the Leptoconopinae, to the Forcipomyiinae and Dasyheleinae.

The phylogeny tree (dendrogram) for the Ceratopogonidae would be as follows:

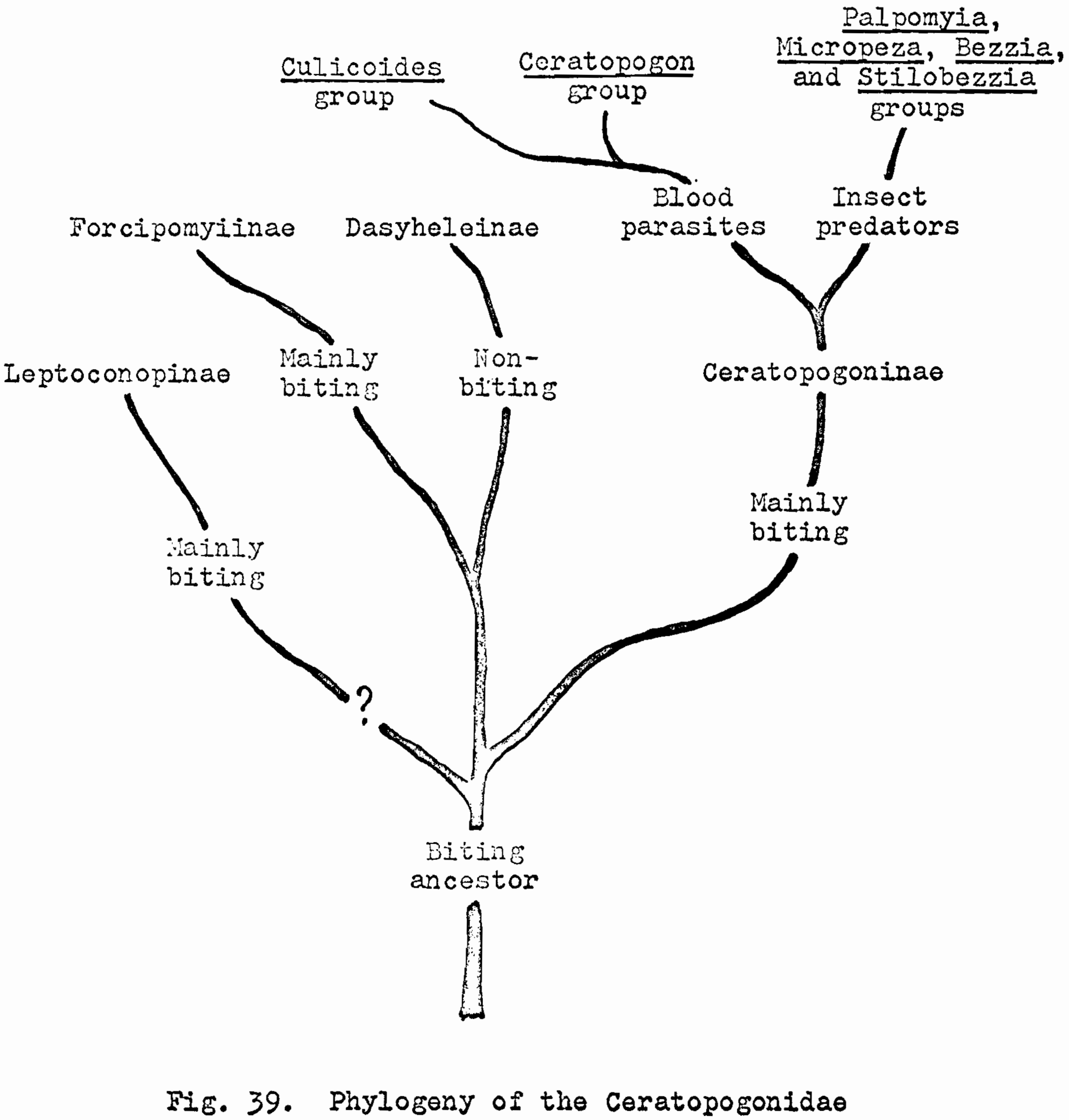


Fig. 39. Phylogeny of the Ceratopogonidae

C. THE FORCIPOMYIINAE

In determining the degree of phylogenetic relationship in any taxonomic group the problem of deciding which characters are specialized and which are primitive must be faced. One of the most general laws of evolution, the law of unequal development or what has recently been called as "Watson's Rule" by de Beer (1954) (vide Hinton, 1958) must not be overlooked, i.e. "not only do different groups evolve at different rates but within any group the organ systems themselves evolve at different rates". This is why most animals are such mixtures of specialized and primitive features and this obviously makes the task of the systematic phylogenist extremely difficult.

1. PRIMITIVE AND ADVANCED CHARACTERS

Before considering the phyletic relationship between the Forcipomyiinae and other subfamilies and between the genera and subgenera in the Forcipomyiinae, it is necessary to consider which characters are primitive and which advanced. This is by no means easy as no systematists of these insects have so far examined and discussed in detail this important topic. An attempt is here made on some of the important characters.

In this discussion, characters are considered primitive when they occur repeatedly throughout the order. More of these are expected to be found in groups that have been established as more primitive, e.g., in the Diptera more primitive characters are found in the Nematocera than in the Brachycera or Cyclorrhapha.

(a) LARVA

(i) Pseudopods (Prolegs).- The pseudopods which characterize the subfamily Forcipomyiinae have been used as important taxonomic characters by Saunders (1956) in his subgeneric division of Forcipomyia. Hinton (1955) has shown these to be secondary adaptive structures not serially homologous with the thoracic legs, and within the Diptera they have been independently evolved at least 27 times. Hinton (loc.cit.) has shown also that the more complex their structure and the more they come to resemble thoracic legs, the more they have departed from their ancestral form. The common ancestor of recent Diptera, according to Hinton (1955) has secondarily lost the thoracic legs and in conformity with Dollo's law or generalization, no recent dipterous larvae have re-evolved such an apparatus.

In the Forcipomyiinae, the prothoracic proleg is undivided, cushion-shaped, bearing few to many hooklets arranged in one or more rows, or divided with each ramus bearing a circlet, or one or more rows, of hooklets. The undivided condition is obviously the simpler and accordingly, more primitive. It also follows that the fewer the number of hooklets there are the more primitive is the type of proleg. The most primitive condition in the subfamily is found in Lasiohelea (Dacnoforcipomyia) anabaenae where only two hooklets are found on the undivided prothoracic pseudopod. The same reasoning would apply to the anal pseudopod and again the most primitive condition is found in Lasiohelea (Dacnoforcipomyia) anabaenae. The most advanced condition is the divided condition found only in Forcipomyia (Schizoforcipomyia) species of which the larvae of only one species, lerouxi, has been described.

(ii) Antenna.- The reduced antenna is considered an apomorphic (specialized) character and the long, well-developed antenna as plesiomorphic (archaic) since in all higher forms in the order the antenna is reduced or absent.

(b) PUPA

(i) *Retention of exuviae*.- This is probably a plesiomorphic character which separates the Forcipomyiinae from the rest of the Ceratopogonidae, but within the Forcipomyiinae some forms do not retain the last larval skin. Retention of the last larval skin could however be a specialized feature since it approximates to similar conditions in higher Diptera, e.g. Stratiomyidae (Brachycera) and all Cyclorrhapha where the pupae are encased in the last larval skin which has become the puparium or cocoon. Obviously, functionally, these more highly evolved pupae are less capable of mobility due to great internal metamorphic changes at this stage and are at the same time most vulnerable.

(ii) *Male sexual processes*.- The position of these processes is either dorsal or ventral. In the Forcipomyiinae the ventral position is found in *Atrichopogon*, the *Lasiohelea* group (*Lasiohelea* s. str., *Dacnoforcipomyia*, Lane's *Lasiohelea stylifer* Lutz, *Thyridomyia*, *Synthyridomyia*), *Trichohelea* and *Neoforcipomyia*, and the dorsal position is found in the remaining genera and subgenera. The condition in *Pterobosca* and *Parapterobosca* however is unknown since their early stages still remain undiscovered. The ventral condition is found in the more primitive Chironomidae and Thaumaleidae and would appear therefore to be the more primitive condition, but is retained in the presumably more advanced Dasyheleinae, Ceratopogoninae and Leptoconopinae.

(c) ADULTS

(i) *Antenna*.- In the Ceratopogonidae the number of segments in the antenna varies, but typically it is 14. The first two segments, scape and pedicel, however, are always constant; only the number of flagellar segments vary. In the Leptoconopinae the number of flagellar segments vary from 9 to 11. In all the remaining midges it is usually 12, but in some Trichohelea species it is only 8, the first four having become secondarily reduced and fused with the pedicel. Since the basic number of antennal segments is three, and an increase in number appears to result from secondary subdivisions of one primary flagellar segment (Snodgrass, 1935) due to a functional need for increasing the surface area available for sense organs (Schneider, 1964), the more segments there are, the more advanced they are likely to be, unless reduction in numbers is a secondary modification. The Leptoconopinae in this respect would be more primitive than the other groups. It also follows from the above that species with elongate distal flagellar segments are more apomorphic in this character than those with less elongate distal segments. In other words, the condition where the individual flagellar segments are elongate is the more highly evolved one than the one with short segments.

(ii) Maxillary palp.- The maxillary palp in the midges is typically five-segmented, but may be four-segmented, the first two or last two segments in the latter condition becoming fused. Since in the Diptera the evolutionary trend is towards reduction in number of the palpal segments (Nematocera typically 5 or 4 - segmented; Brachycera 2 or 1-segmented and Cyclorrhapha 1-segmented) the primitive condition in the Ceratopogonidae is therefore 5-segmented. In the Leptoconopinae, the 4-segmented condition with tendency towards a 3-segmented condition (segments 1 and 2 being usually short and poorly defined) is advanced. So is the 4-segmented condition in Dasyheleinae where segments 1 and 2 are fused, advanced.

(iii) Spermatheca.- In female ceratopogonids, the number of spermathecae varies from one to three. In the last case usually one is vestigial and the other two well-developed. Snodgrass (1935) believes that the paired condition is primitive and the single condition, found in most insects, advanced. Whether the triple condition is more advanced or more primitive than the paired condition is uncertain.

(iv) Male genitalia.- (a) Parameres:- In the ontogenetic development of the parameres, Snodgrass (1957) has shown that they were originally derived from a single pair of phallic lobes, each of which becomes an outer and an inner lobe, the outer lobes giving rise to the parameres. The parameres primarily are 1-segmented but secondarily in their development they may become 2-segmented (Snodgrass, loc.cit.). Although ontogeny does not necessarily recapitulate phylogeny, it may be assumed that the primitive condition is 1-segmented (e.g. Dermaptera, Hemiptera). In the 2-segmented condition the more primitive one would be one in which the telomere is considerably smaller and shorter than the basimere and in which the basimere is also typically short and thick (e.g. Megaloptera, Mecoptera, Trichoptera). In the Ceratopogonidae, the telomere is usually shorter, but may be as long as or longer than, the basimere. In the more advanced Culicidae (e.g. Anopheles species) the telomeres are usually as long as or longer than the basimeres. In the Ceratopogonidae the basimeres are predominantly short and wide, especially in the Leptoconopinae and Dasyheleinae where the telomeres are also typically short and somewhat wide. These plesiomorphic characters are retained in most of the groups but evolutionary tendency towards the apomorphic elongated, narrow condition of both parameral segments can be observed in several lines in most groups, especially in the Forcipomyiinae and Ceratopoginae.

In the Forcipomyiinae the primitive condition is typical of Proforcipomyia, Forcipomyia s. str. and Schizoforcipomyia species. Tendency towards elongation of the parameres is found in Atrichopogon species where both primitive and advanced conditions are found, and also in Thyridomyia and Synthyridomyia species, but in Lasiohelea s. str., Neoforcipomyia and Trichohelea species the more advanced condition is typical. This more advanced condition is also found in Warmkea species.

(b) Parameral claspettes:- Parameral claspettes are secondary structures arising from the mesal surfaces of the basal segments of the parameres (claspers) performing some function at copulation. These have for a long time been erroneously regarded as "parameres" by dipterists "without checking on their credentials" (Snodgrass, 1957). In the lower insects these structures are absent but in the Diptera they are variously modified. In the Blepharoceridae and Tabanidae structures of a similar nature and function, but not homologous to the Nematocerous claspettes, are formed. These are the "paraphyses" of Snodgrass (1957), commonly referred to as "gonapophyses".

In the Ceratopogonidae, the first sign of the development of claspettes is found in Atrichopogon where it is absent in some species. In other groups it is variable in shape and size and becomes greatly modified but generally taxonomically typical of each group. In fact, the evolutionary trends in the development of the claspettes can be observed to originate from the basic, presumably prototypic, organization found in Atrichopogon. The general conclusion concerning claspette phylogeny is that the more complicated the structures are the more advanced they are likely to be. The condition in Atrichopogon is naturally regarded as the most primitive. The evolutionary trends in claspette development in the whole family are shown in Figs. 40, 40a, 40b.

(v) Aedeagus.- Principally two types of aedeagus are found in the Ceratopogonidae, the bipartite condition and the single united condition. The former condition is found in many species of the Lasiohelea group and typical of Stilobezzia species in the Ceratopogoninae, and occur again and again in all groups of the family. Even in the single condition the bipartite nature of the aedeagus is almost always visible. The bipartite condition is therefore considered primitive and the single condition derivative or apomorphic. Snodgrass (1957) has shown that the aedeagus is developed from the union of originally paired mesomeres (inner lobes of phallomeres). Besides, the primitive Ephemeroptera have paired penes which in the Thysanura unite to form a simple median penis, assuming that the penis rudiments in Ephemeroptera are homologues of the phallic lobes in other insects which appears to be the case.

In the Dasyheleinae the typical aedeagus is derived from the bipartite condition through union at the proximal end by formation of the basal arch across the aedeagus just below the basal arms. In many Culicoides species the united condition is formed by union of the distal ends of the bipartite sclerites.. This condition evolves to the more advanced condition where it is shield-shaped or narrowly elongated (e.g. most Forcipomyia s. str. species). In the more advanced Culicidae, e.g. Anopheles species, it is even narrower and more elongated.

2. EVOLUTIONARY TRENDS IN CLASPETTE DEVELOPMENT

The probable evolutionary trends in claspette development within the Forcipomyiinae is shown and summarized pictorially in Fig. 40, and in the Dasyheleinae and Ceratopogoninae in Figs. 40a, 40b (Appendix).

In the Atrichopogon - Thyridomyia - Dacnoforcipomyia - Lasiohelea s. str. line, the development of claspette processes begins in Thyridomyia at the third prototype stage of the plesiomorphic Atrichopogon condition (A_{3a}). The processes are in the form of triangular membranous plates (T_1). These are later lost (T_2, T_3) or thin out and become united to form the membranous flange in Dacnoforcipomyia anabaenae (D_1). From this it is lost and the rounded arch-like condition in some Lasiohelea s. str. species (L_1) is formed. The latter gives rise to the square-topped condition in other Lasiohelea species (L_2).

In the closely related Synthyridomyia and somewhat more distantly related *Trichohelea*, the trend of claspette development begins at a hypothetical stage beyond the *Atrichopogon* third prototype stage (A_{3c}) and proceeds towards the posterior extension of the bases of the claspettes to form the club-shaped (S_{1a}, S_{1b}) or spoon-shaped processes (Tr_1), characteristic of these two groups respectively.

In *Neoforcipomyia* the trend is towards concurrent posterior extension of the bases of the basal arms and inward growth and union of the basal union of the arms. It begins at a hypothetical stage beyond the third *Atrichopogon* prototype stage (A_{3b}).

In the *Atrichopogon* - *Calo*$\overset{f}{c}$*orcipomyia* - *Proforcipomyia* - *Schizoforcipomyia* line, claspette development does not involve the formation of processes (except rudimentary ones in the last stage of *Proforcipomyia*) but the gradual elongation and thinning out of the basal arms to meet abruptly at their apices. An inverted V-shaped arch is thus formed. This, as in *Lasiohelea* s. str. gradually rounds up at the top and eventually becomes square-topped. The *Profoorcipomyia* condition thus parallels that in *Lasiohelea* s. str.

In the *Forcipomyia* - *Metaforcipomyia* - *Warmkea* line, the trend is towards development of claspette processes at the apical ends of the basal arms, either abruptly or smoothly, and subsequent fusion of the processes in various degrees and at various levels. The *Forcipomyia* s. str. type is derived from the *Atrichopogon* fourth prototype condition (A_4), the *Metaforcipomyia* type from the *Forcipomyia* s. str. early stage (F_1) through complete fusion of the processes (M_1) and the *Warmkea* type from the predominant *Forcipomyia* s. str. type (F_{3a}) through the tips of the processes becoming hooked outwardly (W_1).

Fig. 40. Evolutionary trends in the development of claspettes in the Forcipomyiinae

Absent -- *Atrichopogon incultus* Ewen (1958); etc.

A_1 -- *Atrichopogon longicornis* Ewen (1958); *A*. *armaticaudalis* Tokunaga & Murachi (1959); *A*. *flavenicruris* Tokunaga & Murachi (1959); etc.

A_2 -- *Atrichopogon maculosus* Ewen (1958); *A*. *tuberculatus* Ewen (1958); *A*, *jejunus* Macfie (1934); etc.

A_{3a}-- *Atrichopogon humicolus* Ewen (1958); *A*. *corpulentus* Ewen (1958); *A*. *citrinipes* Kieffer (1922); *A*. *bifidus* Ewen (1958); *A*. *crinitus* Ewen (1958); *A*. *inconspicuus* Ewen (1958); etc.

A_{3b}-- *Atrichopogon lewis* (Coquillett) (1901) (Wirth's 1952 figure, not Ewen's 1958 figure); *A*. *okinawensis* Tokunaga (1962); etc.

A_{3c}-- *Atrichopogon remigatus* Ewen (1958); *A*. *sauteri* Ewen (1958); etc.

A_4 -- *Atrichopogon snyderi* Tokunaga (1959); *A*. *raripilipennis* Tokunaga & Murachi (1959); etc.

C_1 -- *Caloforcipomyia squamianulipes* (Tokunaga & Murachi) (1959);

C_2 -- *Caloforcipomyia caerula* (Saunders) (1956)

C_3 -- *Caloforcipomyia varicolor* (Saunders) (1956)

D_1 -- *Lasiohelea* (*Dacnoforcipomyia*) *anabaenae* (Chan & Saunders) (1965)

F_1 -- *Forcipomyia* (*Forcipomyia*) *bikanni* Chan (1965); *F* (*F*.) *securis* Chan (1965); *F* (*F*.) *cinctipes* (Coquillett) (1905); *F* (*F*.) *fascicornis* Tokunaga (1962); *F* (*F*.) *mira* Johannsen (1931); etc.

F_{2a}-- *Forcipomyia* (*Forcipomyia*) *bipunctata* (Linnaeus) (1767); *F* (*F*.) *bipunctatapropinqua* Chan (1965); *F* (*F*.) *fascicauda* Tokunaga (1940); etc.

F_{2b}-- *Forcipomyia* (*Forcipomyia*) *edgari* Tokunaga & Murachi (1959); *F* (*F*.) *hikosanensis* Tokunaga (1940); etc.

F_{3a}-- *Forcipomyia* (*Forcipomyia*) *townesi* Wirth (1952); *F* (*F*.) *squamipes* (Coquillett) (1902); *F* (*F*.) *ingenua* Macfie (1934); *F* (*F*.) *swezeyana* Tokunaga & Murachi (1959); etc.

F_{3b}-- *Forcipomyia* (*Forcipomyia*) *occidentalis* Wirth (1952); etc.

Fig. 40. Evolutionary trends in the development of claspettes in the Forcipomyiinae

F_{4a} -- *Forcipomyia* (*Forcipomyia*) *esakiana* Tokunaga (1940); *F*.(*F*.) *tuthilli* Tokunaga (1959); *F*.(*F*.) *flavitibialis* Tokunaga & Murachi (1959); *F*.(*F*.) *gressitti* Tokunaga & Murachi (1959); etc.

F_{4b} -- *Forcipomyia* (*Forcipomyia*) *raleighi* Macfie (1938); etc.

L_1 -- *Lasiohelea* (*Lasiohelea*) *intermedia* (Saunders) (1964); *L*.(*L*.) *attenuata* (Saunders) (1964); *L*.(*L*.) *flavescens* (Saunders) (1964); *L*.(*L*.) *longicornis* Tokunaga (1940); *L*.(*L*.) *carolinensis* Tokunaga (1940); etc.

L_2 -- *Lasiohelea* (*Lasiohelea*) *cornuta* (Saunders) (1964); *L*.(*L*.) *longineura* (Saunders) (1964); *L*.(*L*.) *uncuspromissa* Chan (1965); etc.

M_1 -- *Metaforcipomyia cerifera* (Saunders) (1956)

N_1 -- *Neoforcipomyia* spp.

P_1 -- *Proforcipomyia setigera* (Saunders) (1959)

P_2 -- *Proforcipomyia bromeliae* (Saunders) (1956)

P_3 -- *Proforcipomyia yapensis* (Tokunaga & Murachi) (1959); *P*. *sauteri* (Kieffer) (1912); *P*. *mortuifolii* (Saunders) (1959); *P*. *clara* Chan (1965); *P*. *pennielongata* Chan (1965); etc.

P_4 -- *Proforcipomyia wirthi* (Saunders) (1956); *P*. *calcarata* var. *sonora* (Wirth) (1952); etc.

S_{1a} -- *Lasiohelea* (*Synthyridomyia*) *colemani* (Wirth) (1952); *L*,(*S*.) *murinus* (Winnertz) (1852); etc.

S_{1b} -- *Lasiohelea* (*Synthyridomyia*) *unituberculata* (Tokunaga) (1959)

Sc_1 -- *Forcipomyia* (*Schizoforcipomyia*) *fuscimanus* (Kieffer) (1921)

Sc_2 -- *Forcipomyia* (*Schizoforcipomyia*) *lerouxi* Chan (1965)

Sc_3 -- *Forcipomyia* (*Schizoforcipomyia*) *fuscimaculata* (Hardy) (1960)

T_1 -- *Lasiohelea* (*Thyridomyia*) *monilicornis* (Coquillett) (1905); *L*.(*T*.) *palustris* (Saunders) (1925); etc.

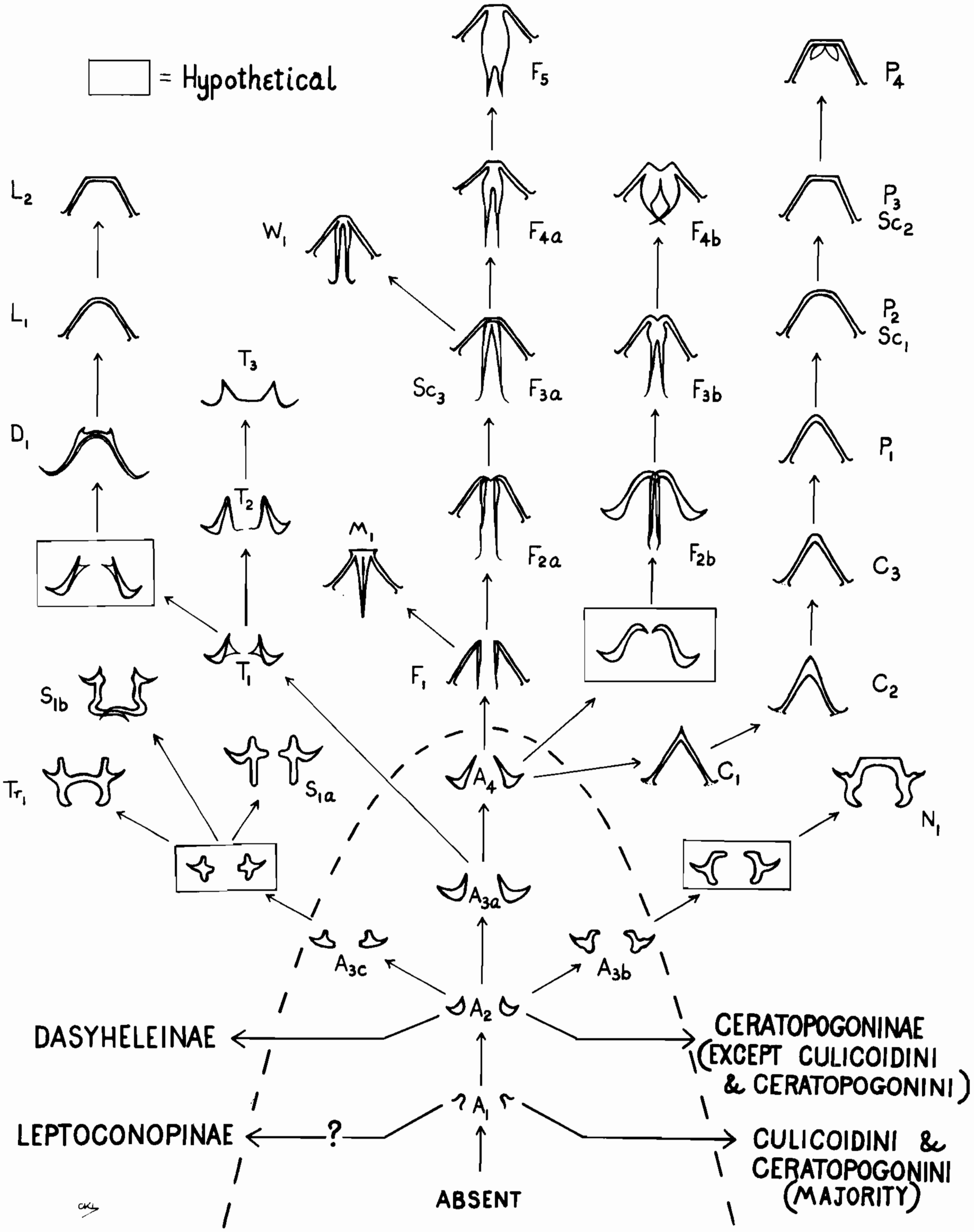
T_2 -- *Lasiohelea* (*Thyridomyia*) *rugosa* Chan (1965); *L*.(*T*.) *aspinosa* (Saunders) (1956); etc.

T_3 -- *Lasiohelea* (*Thyridomyia*) *gossympina* Chan (1965)

Tr_1 -- *Trichohelea* spp.

W_1 -- *Forcipomyia* (*Warmkea*) spp.

Fig. 40. Evolutionary development of claspettes in the Forcipomyiinae



The *Schizoforcipomyia* type presumably is also derived from one of the early *Forcipomyia* s. str. types (F_{2a}) having arisen, very probably, in the same way as in the *Proforcipomyia* (P_2, Sc_2). Those arising with *Proforcipomyia* presumably also share the common single spermatheca in the adult female while those arising with *Forcipomyia* s. str. presumably also retain the common two spermathecae.

3. SYSTEMATIC POSITION OF THE FORCIPOMYIINAE

The Ceratopogonidae has been classified by most recent authors into four natural groups, currently accepted as monophyletic: the Genuine Group (Forcipomyiinae), the Intermediate Group (Dasyheleinae), the Vermiform Group (Ceratopogoninae) and the Musciform Group (Leptoconopinae). Of these the Forcipomyiinae are very likely the most primitive. Their larval basic general features run through several of the more primitive nematocerous groups. For example, the larvae of Phlebotominae, Thaumaleidae, Chironomidae and Dixidae all have the hypognathous head, three thoracic segments and eight abdominal segments, the body bearing generally a prothoracic proleg and an anal pseudopod. This common basic general morphological feature is indicative of a common early ancentry. Besides, the ecological habitats of the ceratopogonid groups show a gradation from truly terrestial (most Forcipomyiinae) through semi-aquatic (most Dasyheleinae) to purely aquatic forms (most Ceratopogoninae and Leptoconopinae). Consistent with the basic assumption that insects were originally terrestial and secondarily aquatic, this would place the Forcipomyiinae at a comparatively more primitive level than the other groups. Based on larval morphology and ecology, therefore, the vermiform and musciform groups would be at a more advanced level, with the Dasyheleinae occupying an intermediate position and the Forcipomyiinae the most primitive.

However, consideration of the feeding habits of adult Ceratopogonidae does not clearly show that the Forcipomyiinae is the most primitive group. Assuming that Downes' (1958) conclusion that the biting forms are more primitive than the non-biting forms in the Diptera and other biting flies, it follows that a group in which the females have a wide range of biting habits and hence a wide range of hosts, will necessarily be more primitive than one in which the range is less wide. This of course also assumes that host adaptation with respect to the feeding habit within the family progresses approximately at the same rate. In the Forcipomyiinae, the biting habit is common among many species and the hosts attacked range from insects to arachnids, amphibians and mammals. *Neoforcipomyia* species, for example, attack lepidopterans, phasmids, tipulids, culicids, neuropterans, and dragonflies (Wirth, 1956). Some *Forcipomyia* s. str. species attack sawfly and lepidopterous larvae. *Pterobosca* species attack dragonflies and lacewing flies (Wirth, 1956; Tokunaga, 1959). *Lasiohelea* s. str. species suck amphibian blood, e.g. *L. velox* and *L. fairfaxensis* feed on frogs (Pechuman and Wirth, 1961) and one Malaysian species (unidentified) feed on the toad *Bufo asper* (Yuen, 1962 and pers. observation), presumably transmitting the filaria *Icosiella innominata* Yuen. *Lasiohelea* (*Dacnoforcipomyia*) *anabaenae* feeds on human blood (Chan and Saunders, 1965). According to Tokunaga

(1937a) and Mayer (1955a) some Lasiohelea s. str. species feed on cattle. Atrichopogon (Melohelea) species attack meloid beetles and according to Downes (1958) a species was found on the wings of a moth, another on mealy bugs and two records on mammals. Atrichopogon (Atrichopogon) pollinivorus Downes obtains the blood meal analogue from pollen grains (Downes, 1955).

The other group which also has a wide range of hosts is the monotypic group Culicoides whose hosts range from reptiles (turtles, lizards) to birds, and mammals (cattle, man) (Downes, 1958). The wide range of hosts in Culicoides shows that the latter's association with its hosts must have been ancient.

It is interesting to note that in the Ceratopogonidae, the two groups Forcipomyiinae and Ceratopogoninae, show close parallelism in feeding habits. In the Forcipomyiinae, Lasiohelea species feed mainly on vertebrate blood and Neoforcipomyia, Pterobosca, Atrichopogon (Melohelea) and some Forcipomyia species feed mainly on insect blood. In the Ceratopogoninae, Culicoides species parallels Lasiohelea species in their vertebrate blood-sucking habit and the remaining tribes parallel the insectivorous Forcipomyiinae, but in this case they are not parasites but predators.

Downes (1958) believes that Leptoconops is closer to Culicoides than is commonly supposed and most authors believe that the Dasyheleinae are closer to the Forcipomyiinae than the other subfamilies. But since the Leptoconopinae are typically biting forms and the Dasyheleinae may be wholly non-biting, it would therefore appear that, by recency of ancestry, the Ceratopogoninae would be more primitive than the Forcipomyiinae, i.e. assuming that the biting habit is more primitive.

If this were the case, then the terrestial habitat of Forcipomyiinae larvae and pupae would be a secondary one but this is contrary to present knowledge. No case of reinvasion of land by aquatic forms in the Forcipomyiinae is known but the reverse is the case in *Trichohelea* and *Warmkea* species. The Forcipomyiinae, all points considered, would therefore still be likely the most primitive group in the Ceratopogonidae. It would appear then that somewhere along the line in the evolution of the presumably biting ancestor of the Ceratopogonidae, the non-biting habit emerged (presumably from the ability to adapt to a blood meal analogue from plants, e.g. *Atrichopogon pollinivorus*, while the biting habit continued to be retained in most of the representative groups.

(a) Phylogenetic Relationship between Groups in the Forcipomyiinae

In the present study phyletic relationship between the genera and subgenera in the Forcipomyiinae is approached principally from comparative morphology of all stages, other evidence, e.g. ecological, genetical, cytological and physiological, being too scanty to provide adequate grounds for consideration. The evolutionary trends within the group, however, are resolved primarily, not exclusively however, from studies on the adult male genitalia mainly because genitalic characters have been found by most authors to be reliable taxonomic characters in identifying the genera and subgenera in all groups of the family.

(i) The *Lasiohelea* Group and *Atrichopogon*.- In the Forcipomyiinae phylogenetic relationship between some of the genera and subgenera has been generally commented upon in discussions on the genera *Atrichopogon* and *Lasiohelea* (*Thyridomyia*). For the sake of clarity, it is presented briefly again here. From comparative morphology, the groups Lasiohelea, Dacnoforcipomyia, Thyridomyia, Synthyridomyia and new subgenus (represented by Lane's Lasiohelea stylifer Lutz) are considered most closely related to one another than to the rest of the Forcipomyiinae. The genus Atrichopogon shows many morphological similaries in all stages with this group but in many characters appear to be more plesiomorphic than the Lasiohelea group and in a few other characters more apomorphic.

Downes (1958) has mentioned that it is difficult to decide whether the early Diptera were originally predators of vertebrates or of insects since Tillyard (1935) has shown that when they originated in the Permian, terrestial forms of both groups were available. Well-established biting forms of Lasiohelea species are known to be vertebrate blood-suckers, and those of Atrichopogon species to be predominantly insect blood-suckers, although there have been records of mammalian blood-suckers. If the latter cases were confirmed to be true, it would suggest that insect blood-sucking is more primitive than vertebrate blood-sucking. From zoogeographical considerations and genitalic studies this conclusion appears to be sound since in the latter case the Lasiohelea type of claspettes can be shown to have been derived from the plesiomorphic Atrichopogon type.

(ii) Neoforcipomyia.- Neoforcipomyia, like Atrichopogon, is closest to the Lasiohelea group from comparative morphology of all stages. The larvae of Neoforcipomyia share with the Lasiohelea group many common, more or less typical characters: the comparatively small, strongly hypognathous head, four or fewer low prominences on vertex, presence of ocular seta, small but normal antennae, undivided prothoracic pseudopod with anterior row of hyaline, and posterior row of sclerotized, hooklets; posterior pseudopod with nine pairs of hooklets arranged in two rows. The pupae of Neoforcipomyia also share with the Lasiohelea group several common features: the ventral position of the male sexual processes; three pairs of tubercles on the head sclerites, the anterior pair typically setate; tubercles on body small to rudimentary. The adults also share with the Lasiohelea group many common characters: in the female, basal flagellar segments subspherical, distinctly shorter than ultimate five segments and never flask-shaped; maxillary palp completely segmented; hind TR larger than 2.4, wings unadorned, rather densely haired with slender macrotrichia; costa distinctly beyond middle of wing, second radial cell narrow, long, and at least as long as first; first radial cell obliterated and slit-like. In the male, Neoforcipomyia shares with the Lasiohelea group most of the common characters as in the female, and even in genitalia they resemble one another in the shape of the parameres and relative lengths of the ninth sternite and tergite. There is therefore no doubt about their close affinity.

(iii) Trichohelea.- The systematic position of Trichohelea is difficult to determine. It has many characters peculiar to itself in the subfamily. Its larvae are different from all other Forcipomyiinae in the dorso-ventrally flattened head with reduced antennae. This however is a secondary adaptation to living submerged in water between closely appressed leaves of plants. The pupa is also distinct from other Forcipomyiinae in the presence of lateral seta in the generally parallel terminal processes which condition is also found in the chironomid subfamily Podonominae (e.g. Lasiodiamesa species), thus showing a remote common ancestry with the chironomids. The males differ from males of other Forcipomyiinae in lacking empodia between the claws and in some species the females have 10 antennal segments instead of the usual 14. In addition to these distinguishing characters, Hardy (1960) pointed out that in T. brevis and perhaps in other species (which he had no occasion to examine) the wing alula is bare instead of typically fringed. He (loc. cit.) therefore considers Trichohelea a distinct genus in terms of Saunders' (1956) criteria for subgeneric classiciation of Forcipomyia. However, Trichohelea in some characters shows that it is more closely related to the Lasiohelea group than to the Forcipomyia group. In the larva, the presence of two types of hooklets (hyaline and sclerotized) on the pseudopods is a plesiomorphic character of the Atrichopogon-Lasiohelea-Neoforcipomyia group. In the pupa, the ventral position of the male sexual processes is similarly a plesiomorphic character of the group. In the male adult genitalia, the general facies, e.g. slender, rather elongate parameres, are also typical of the group. The H-shaped claspettes can be shown to be derived from one of the plesiomorphic conditions of the Atrichopogon claspettes, and in this sense, it is closer to the Synthyridomyia 'club-shaped' type than any other type, except perhaps the Neoforcipomyia type.

It would appear therefore that Trichohelea was an early offshoot in the phylogeny of the Forcipomyiinae and its adaptation to an aquatic environment in the early stages has brought about divergent morphological characters from the group.

(iv) Proforcipomyia and Caloforcipomyia.- In the Forcipomyia line of evolution it can be easily shown, from comparative morphology, as for the Lasiohelea-Atrichopogon-Neoforcipomyia group, that Proforcipomyia and Caloforcipomyia are more closely related to each other than to Forcipomyia s. str. Warmkea, Schizoforcipomyia or Metaforcipomyia. Their larvae are more elongate than the other groups and share many common characters: simple spinulose cushion-shaped prothoracic pseudopod; long somewhat curved antennae; a hairs slightly modified from the spear-shaped type of Forcipomyia s. str.; last abdominal segment with dorsal chitinous process bearing short to very long setae; cauda longer than other groups and pointed apically; anal blood gills two, bifid. Their pupae are also different from other groups in two distinct common characters: long closely appressed terminal processes of last abdominal segment, and presence of a large pair of setae tubercles generally situated just posterior to the prothoracic horns. In the adult, their common most distinctive character, not present however in all species of Proforcipomyia, is the inverted V-shaped structure of the claspettes.

Comparative morphology in all stages shows that Caloforcipomyia is closer to the Forcipomyia s. str. group than is Proforcipomyia, chiefly in the profile of the larval head, larval head and body chaetotaxy, nature of pupal respiratory horns, the more elongate and narrower basimeres of the adult genitalia. From consideration of the phylogeny of genitalic structures (Fig. 40) it follows that Caloforcipomyia and Proforcipomyia as a monophyletic group are paraphyletic to the monophyletic group comprising Forcipomyia s. str. Warmkea, Schizoforcipomyia, and Metaforcipomyia.

(v) Warmkea.- In the last four groups, Warmkea is probably nearest

Forcipomyia s. str. although its larvae and pupae have diverged in morphological characters from the typical through adaptation to an aquatic habitat. Saunders (1956) who is most familiar with this subgenus, considers it a "young" offshoot from the parent stock of *Forcipomyia*. This is apparently correct from the basically identical genitalic structures and from the retention, in the larvae, of spear-shaped *a* hairs, among other minor characters.

(vi) *Schizoforcipomyia*.- *Schizoforcipomyia* is also undoubtedly very close to *Forcipomyia* s. str. and a very "young" offshoot of the parent stock of *Forcipomyia* s. str. In larval characters it is more primitive in antennal structure than *Forcipomyia* s. str. but more advanced in pseudopodal structures. In adult morphology it is typically Forcipomyian except for the aedeagus and claspettes (only in *lerouxi*) in the male. Whether it or *Warmkea* is closer to *Forcipomyia* s. str. is thus hard to determine. If Tokunaga and Murachi's (1959) "subgenus B" is confirmed to be *Schizoforcipomyia*, then it could be assumed that the shape of the aedeagus is variable but the two terminal hook-shaped sclerites are constant characters of the subgenus. If this be the case, then *Schizoforcipomyia* is intermediate between *Forcipomyia* s. str. and *Proforcipomyia* but closer to the former and closer to *Caloforcipomyia* than *Proforcipomyia*. Between *Forcipomyia* s. str. and *Caloforcipomyia*, *Schizoforcipomyia* appears to be decidedly closer to the former.

(vii) *Metaforcipomyia*.- *Metaforcipomyia* is known only from one species, cerifera, but the descriptions and drawings of Saunders (1956) for this species show beyond a doubt that it is very close to Forcipomyia s. str., Schizoforcipomyia and Caloforcipomyia. Its male genitalic structures show that it has progressed beyond the more primitive Forcipomyia s. str. species but equivalent to the more advanced Forcipomyia s. str. species. In immature characters it apparently lags behind Forcipomyia s. str., retaining some of the more plesiomorphic features of Proforcipomyia and Caloforcipomyia though decidedly Forcipomyian in body build. Whether it is closer to Forcipomyia s. str., Schizoforcipomyia or Caloforcipomyia is difficult to determine. This can however be easily solved with the discovery of all stages of more species.

(viii) Pterobosca and Parapterobosca.- The phylogenetic relationship of Pterobosca and Parapterobosca with the other groups in the subfamily is hard to determine with morphological evidence only from the adult female. Most characters seem to be adapted for feeding on insect hosts: large, broad leg empodia for adhering to wings of dragonflies or lacewing flies; elongation of one or two additional distal antennal segments from the typical five, to have more surface area available for sense organs (presumably chemoreceptors associated with detecting the presence and location of hosts); large third maxillary palpal segment to house a large deep sensorium, presumably also for hunting hosts; large broad wings with long costa, for more efficient and faster flight. These apparently are apomorphic characters. The generally long second radial cell in the wing places them close to

Lasiohelea and Atrichopogon and their possession of one or two spermathecae would place them nearer Atrichopogon than Lasiohelea, but since wing macrotrichia and venation resemble closer to those of Lasiohelea than Atrichopogon they must be considered as arising from the same parent stock as the Lasiohelea group, or as far back as the parent stock of both the Lasiohelea group and Atrichopogon group. In their biting habit Pterobosca species appear to be closer to Atrichopogon, both genera being largely or wholly insect blood-suckers but Parapterobosca would be closer to Lasiohelea species in its vertebrate blood-sucking habit. Their true systematic position remains to be seen. But since at the same time they possess many of the plesiomorphic characters of Forcipomyia s. str. they can be temporarily considered here as intermediate between the Atrichopogon-Lasiohelea-Neoforcipomyia-Trichohelea line of evolution and the Forcipomyia-Metaforcipomyia-Proforcipomyia-Caloforcipomyia line but closer to the former.

(ix) Forcipomyia s. str. - The parent stock of Forcipomyia s. str. itself can be traced to an Atrichopogon-like ancestor from consideration of male genitalic characters (Fig. 40) and from the fact that at least one Atrichopogon species, crinitus, is exactly alike in head and body chaetotaxy with Forcipomyia s. str. species (Ewen and Saunders, 1958). In A. crinitus, the ocular seta (seta "7" of Ewen and Saunders, 1958), found in all other Atrichopogon species, is lacking and is a distinctly apomorphic character in the evolutionary line of the Forcipomyia groups. In addition, crinitus pupae are "very Forcipomyia-like" (Ewen and Saunders, loc. cit.).

(x) Atrichopogon, the Living Prototype of the Ceratopogonidae.- From all the foregoing considerations, there can be no doubt, therefore, that Atrichopogon species represent the existing prototypic organization of the subfamily Forcipomyiinae and could perhaps even be the real prototype of all ceratopogonoid organization, since in this genus most ceratopogonid evolutionary trends appear in their archaic stages. This conclusion, it should be noted, is contrary to most current conception that Atrichopogon is one evolutionary stage beyond Forcipomyia s, str, as implied, for example, in Macfie's (1932) statement, "It would be best probably to regard Lasiohelea as a subgenus of Forcipomyia and as one stage beyond Euforcipomyia in the direction of Atrichopogon".

The combination of primitive and advanced features in Atrichopogon, with the great diversity in larval and pupal chaetotaxic patterns and variability in shape and size of the antenna, pupal prothoracic horn, degree of bifidity of the larval prothoracic pseudopod and the great variability in number of pseudopod hooklets and the claspette prototype structures of the adult male, is indicative of plasticity and instability in genetic constitution of the genus. This accounts for the ease with which "explosive" radiation from this basic phenotype into the various forms in the family could take place.

The size of Atrichopogon population is presumably small since rapid rate of evolution is often attributed to small populations (Mayr, 1963). Pertinent here is the Sewall Wright principle of genetic drift and random fixation in small populations, permitting rapid speciation. Since this principle is applicable to populations on isolated islands or islands adjacent to land masses (Gressitt, 1961) the most likely original centre of evolution and radiation for Atrichopogon would be in the Oriental Region in or close to the Sundaland.

The phylogeny of the Forcipomyiinae is summarized in the following dendogram:

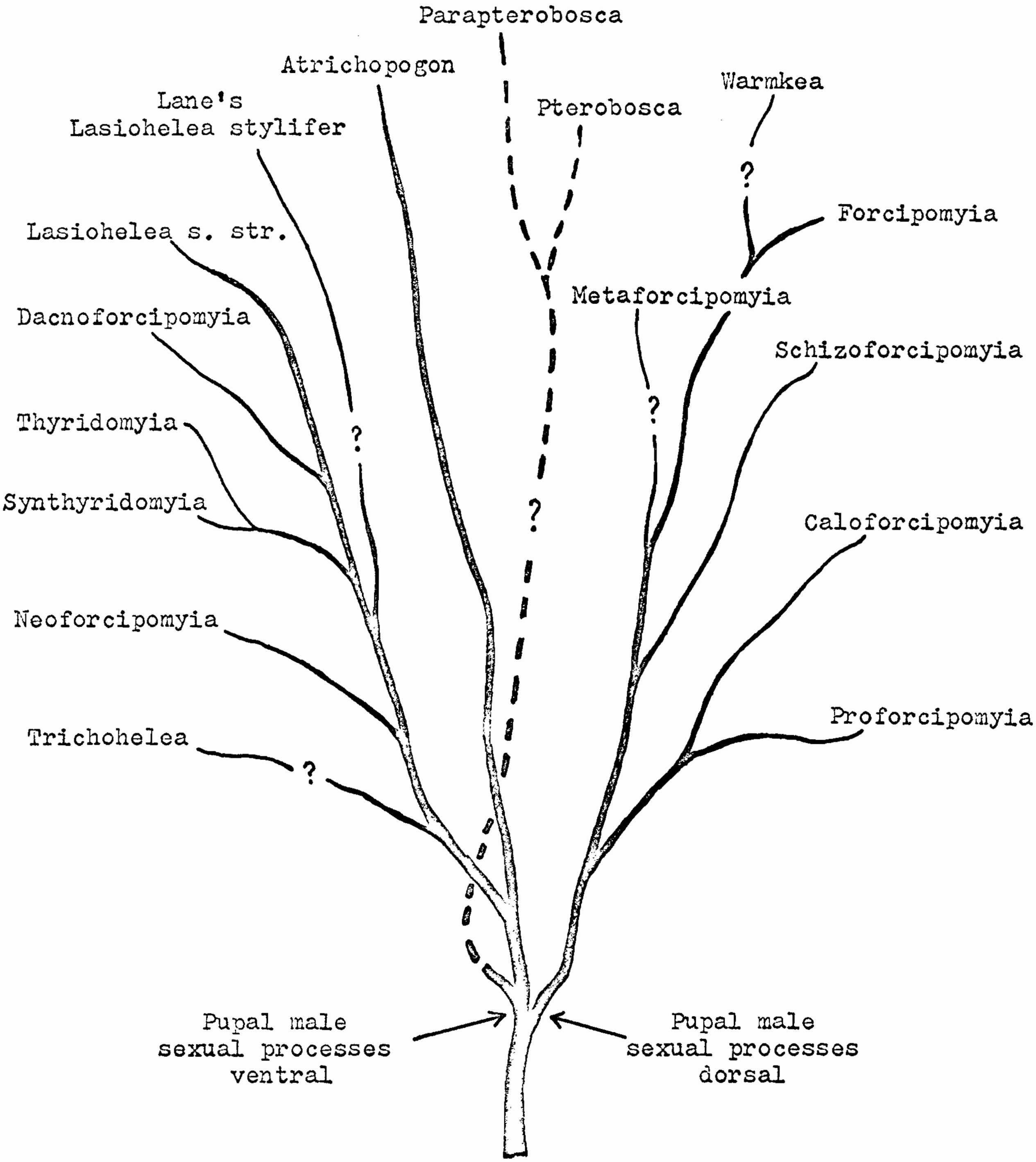


Fig. 41. Phylogeny of the Forcipomyiinae

ECOLOGY

I. INTRODUCTION

Life history studies were carried out on three species of Ceratopogonidae occurring in fair abundance and easily obtainable in a pond at Morgan Arboretum, Macdonald College. No such ecological studies have previously been carried out on these flies. Studies strictly ecological, on the Ceratopogonidae are few and most have been centred mainly on habits, life-cycle, larval habitats, ovarian cycle, sampling methods and daily cycle in relation to meteorological conditions. A review of the literature up to 1962 is given by Kettle (1962) and subsequent ecological papers, do not report quantitative sampling studies for all stages for any species of Ceratopogonidae. A preliminary sampling study according to the method of LeRoux & Reimer (1959) for orchard insects was adopted for the three species under study.

II. STATUS OF THE INSECTS

The three midges selected for these preliminary studies were Palpomyia slossonae (Coquillett), Bezzia glabra (Coquillett) and Dasyhelea grisea (Coquillett) (identified by Wirth). The biology of these three species is unknown except for their life cycle and natural habitat (Thomsen, 1937). Economically they are perhaps unimportant. Their occurrence in fairly large numbers in ponds, streams and other water-holding places like lakes and rivers, in the immature stages, does not normally interfere with human activities but because they are suspected carriers of nematodes and may prove to be intermediate hosts of cattle or other insect parasites, their presence at Morgan Arboretum could prove harmful to cattle which drink water from the pond. The immature stages of these species are not, however, known to be carriers of nematodes or other parasites. The adults of P. slossonae and B. glabra are believed to feed on other smaller insects, some of economic importance, and with those of D. grisea, pollinators of cultivated plants.

III. EXPERIMENTAL PLOT

The experimental plot was an artificial pond (Fig. 42) originally created to provide drinking water for cattle reared on the Macdonald College Farm at Morgan Arboretum. The pond was roughly oval in shape, approximately 600 feet long, 40 feet wide and about 4 feet deep at the centre. Its fauna and flora were relatively rich and stabilized and about three-quarters of its surface covered with blanket algae forming a layer of about five inches just below the water surface. Associated with the algae in various places were decaying grass stems and leaves, and floating with the algae, especially along the edges of the pond, were numerous duckweeds (*Lemma* sp.). In the blanket algae early stages of the three species of midges studied were found. Other organisms found in the same habitat include several species of leeches, at least two species of *Hydra* (green and brown species), crustacea, beetle larvae of at least two species, hemipterans (*Anisops* sp., etc.), mites, enchytraed earthworms, planarians, chironomid larvae of at least four species, tabanid larvae, and *Culicoides* larvae.

The plot was not seriously disturbed except by cattle which came to drink and wild ducks which made infrequent visits. The water level of the pond fluctuated with the rainfall and the seasons, being highest in spring and lowest towards autumn. As the season progressed from spring to summer to autumn the water level receded and algae on the periphery of the pond dried up. However, the pond remained wet in the centre throughout the period May to September, 1964.

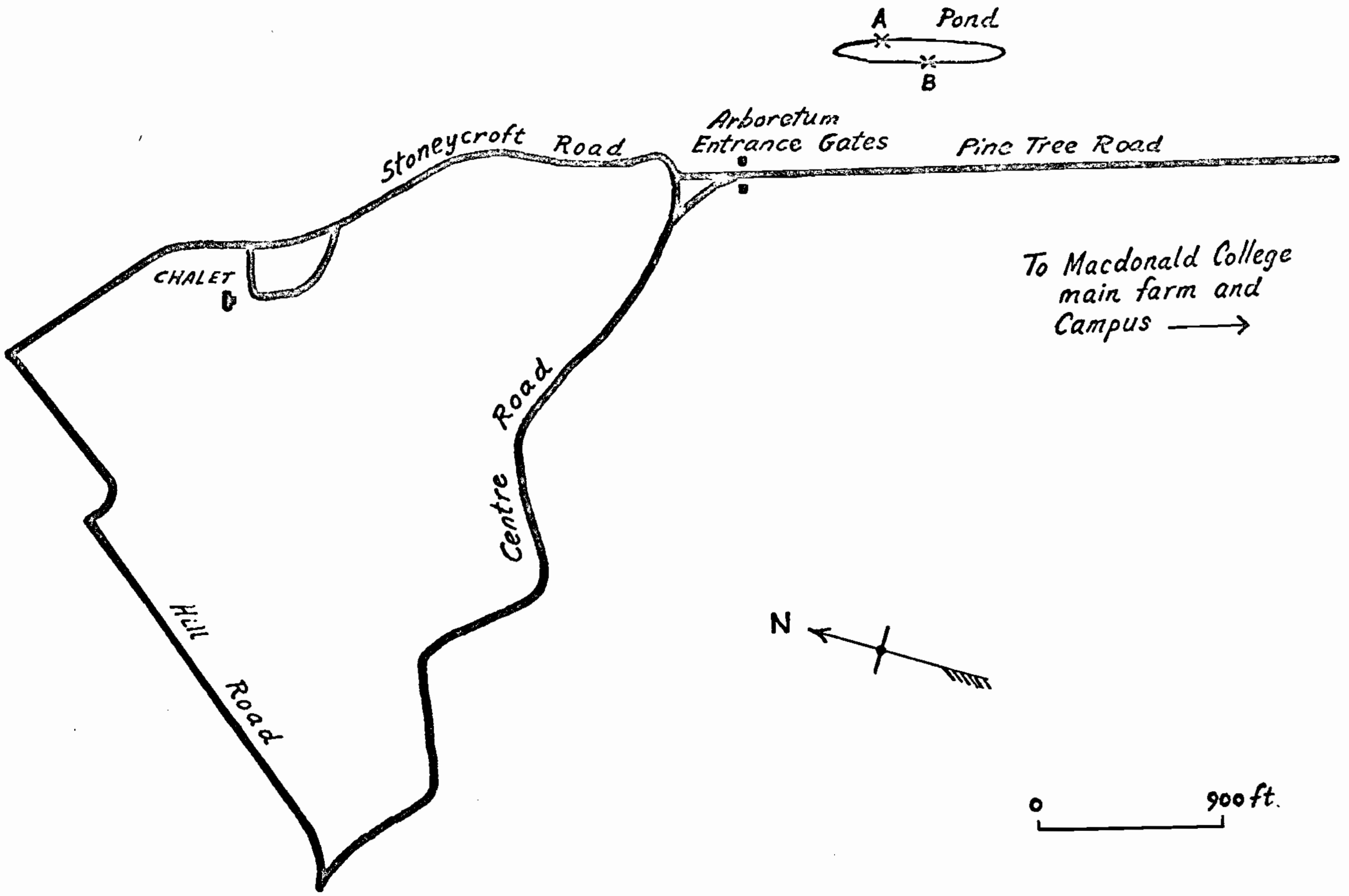


Fig. 42 MORGAN ARBORETUM

IV. SAMPLING PROCEDURE

To study the distribution of the immature stages of the three species, two sites, A and B, separated by about 45 yards (Fig. 42) were chosen. The vegetation at the two sites varied somewhat: that at A was mainly algae and Chlorella and that at B mainly a mixture of algae and decaying grass. The algae at B were growing in water slightly more dirtied by mud and debris. Eggs, larval and pupal stages of the three species were found in greatest numbers in algal samples. These were collected and placed in bottles, 3" x 2¼", and brought back to the laboratory for counting. Mud collected at the bottom of the pond never yielded any significant numbers of larvae, and only a few were observed swimming in the water. Their occurrence in open water is probably indicative of migration or movement associated with predation.

V. SAMPLE UNIT

At each sampling, 20 samples from each site were collected and examined. The time required for one person to examine one sample took, on the average, approximately 20 minutes. Two persons examining and counting 20 samples took approximately seven hours each. Because of the limits of time and man-power (two men) the sample decided upon was 1.41 cc., i.e. a sample unit consisting of algae occupying a volume of 1.41 cc. with a thin film of water. At the beginning of the experiment, in May, this unit yielded on the average four larvae of P. slossonae, three of B. glabra and about one larva of D. grisea and was not considered suitable for statistical analysis but satisfactory to show trends of population changes of the species throughout the growing season.

VI. TIMING OF SAMPLING

Sampling was started on May 13, 1964, and was terminated on September 12, 1964, when sampling became impractical due to the cold weather and extreme muddiness due to the low water level of the pond. All three species were sampled concurrently at intervals of about three days for the first month. During this period, laboratory rearings showed that *P. slossonae* and *B. glabra* each took about a month per stadium and *D. grisea* about one week. Hence, from June 9 onwards, samples were taken once a week and this schedule was maintained for the remainder of the sampling period.

VII. RESULTS

Total counts for each stage of the three species, chironomid species taken collectively irrespective of stage in the samples, per sampling date for the period May 13 to September 12, 1964, are recorded (Tables 3 to 13). Since chironomids constitute the main food source of P. slossonae and B. glabra, and since all species of chironomids are preyed upon, some more than others, the relationship between densities of predator species and prey (chironomid) species was investigated (Fig. 63).

TABLE 3

Seasonal distribution of all stages of P. *slossonae* at Morgan Arboretum, pond site A, May 13 to September 12, 1964.

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 13					16			1	1
18				2	19	5	7		
20				2	29	13	6		
25	300*			2	16	3	4	2	2
27					8	2	4		5
30				1	9			1	1
June 2		1		1	21	3	4		
5					3	3	1	1	
9		133	8	1	31		1	1	
15		85	33	1	4		1	2	
24		7	18	5	11				
30			98	1	4				
July 6			46	2	1				
14		1 0	6	2	2				
20		46	13	6	11	1			
27		24	22	33	13			1	
Aug 3		4	14	22	5				1
10		1	5	12	2				
17		1	10	7	5				
25			14	24	11				
31		1	3	16	19				
Sept 8				3	4				
12		1			5				
Total	300	314	291	145	268	58		19	

Sample size: 28•2 c.c.

* To the nearest 10.

TABLE 4

Seasonal distribution of all stages of P. slossonae at Morgan Arboretum pond, site B, May 13 to September 12, 1964.

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 13			3		2		1		
18				4	39	5	10	2	6
20					21	13	22	6	5
25	100*				4		5	1	1
27	600*	4			4	2	1	3	
30	630*				2	9	5	4	7
June 2	900*			1	1	6	3	4	7
5		154			3	3	1		
9			15		7				
15		8	27	1	3				
24		6	18	2					
30			9						
July 6	250*	29	43	2	2				
14		48	36	5	3				
20		27	7	4	4			1	
27		22	5	1	4				
Aug 3		12	6	18	4				
10		8	7	13	11				
17			20	8	8				
25		3	10	3	4				
31		1	3	10	2				
Sept 8		2		5	4				
1 2				1	6				
Total	2380*	414	213	78	138	86		47	

Sample size: 28.2 c.c.

* To the nearest 10.

TABLE 5

Seasonal distribution of all stages of P. slossonae at Morgan Arboretum pond, sites A and B, May 13 to September 12, 1964.

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 13			3		18		1	1	1
18				6	58	15	17	2	6
20				2	50	26	28	6	5
25	300*			2	20	3	9	3	3
27	600*	4			12	4	5	3	5
30	630*			1	11	9	5	5	8
June 2	900*	1		2	22	9	7	4	7
5		154			6	6	2	1	
9		133	23	1	38		1	1	
15		93	60	2	7		1	2	
24		13	36	7	11				
30			107	1	4				
July 6	250*	29	89	4	3				
14		58	42	7	5				
20		73	20	10	15	1		1	
27		46	27	34	17				
Aug 3		16	20	40	9				1
10		9	12	25	13				
17		1	30	15	13				
25		3	24	27	15				
31		2	6	26	21				
Sept 8		2		8	8				
12		1		1	11				
Total	2680*	728	504	221	387	138		66	

* TO THE NEAREST 10

Sample size : 56.4 c.c.

TABLE 6

Seasonal distribution of B. glabra in all stages at Morgan Arboretum pond, site A, May 13 to September 12, 1964

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 13				3	15				
18				9	18				
20				8	14	2	2		1
25			2		2	1	1	2	
27				1	8	3	3	1	
30					4				
June 2				3	13	1	1		
5					3	3	2	1	2
9		1			2		1	2	4
15		5						1	3
24			1		1				
30	137	12	1		2				
July 6		35							
14		3	6	8	13				
21		6	4	9	9	3		1	
27		4	7	2	11				
Aug 3		4	5	6	1				
10			2	14	5				
17				2					
25		3	5	1	2				
31			5	13	3				
Sept 8			2	13	4				
12		2	6	1					
Total	137	75	46	94	130	23		18	

Sample size: 28.2 cc.

TABLE 7

Seasonal distribution of B.glabra in all stages at Morgan Arboretum pond, site B, May 13 to September 12, 1964.

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 13			2	1	3	1	1		
18				2	1				
20							1		
25				1	1			1	1
27									
30									
June 2							1	1	
5					1	1	1	1	
9		3				1			1
15	275	2							
24		4			1				
30		9							
July 6		32	2	1					
14		4	19	4					
21		17	47	6					
27		1	5		1				
Aug 3			8	19	4		1		
10			6	11	3				
17			1	2	3				
25		3	5	8	11				
31		2	7	2	3				
Sept 8		1	7	7	7				
12			2	3	6				
Total	275	78	111	68	45	8		5	

Sample size: 28.2 cc.

TABLE 8

Seasonal distribution of <u>B. glabra</u> in all stages at Morgan Arboretum pond, sites A and B, May 13 to September 12, 1964.

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 13			2	4	18	1	1		
18				11	19				
20				8	14	2	3		1
25			2	1	3	1	1	3	1
27				1	8	3	3	1	
30					4				
June 2				3	13	1	2	1	
5					4	4	3	2	2
9		4			2	1	1	2	5
15	275	17						1	3
24		4	1		2				
30	137	21	1		2				
July 6		67	2	1					
14		7	25	12	13				
21		23	51	15	9	3		1	
27		5	12	2	12				
Aug 3		4	13	27	5		1		
10			8	25	8				
17			1	4	3				
25		6	10	9	13				
31		2	12	15	6				
Sept 8		1	9	20	11				
12		2	8	4	6				
Total	412	153	157	68	45	31		23	

Sample size: 56.4 cc.

TABLE 9

Seasonal distribution of D.grisea in all stages at Morgan Arboretum pond, site A, May 25 to September 12, 1964.

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 25	43	29				2	1		
27	96	18					2	2	1
30	124	47	2						
June 2	89	5	7						
5		2	34	3					1
9			1	10	1				
15			4	15	5				
24			3	3	6	2	1		
30					2	1	2	1	
July 7									
14		1	3	1					
20				1	11				
27			3	5	8				
Aug 3			2		8				
10									
17		1	1		3				
25			1	1	1				
31			4	4	4				
Sept 8					2				
12			1						
Total	352	101	66	43	56	11		5	

Sample size: 28.2 cc.

TABLE 10

Seasonal distribution of D. grisea in all stages at Morgan Arboretum pond, site B, May 25 to September 12, 1964.

Date	Eggs	Larvae				Pupae		Adults	
		1st instar	2nd instar	3rd instar	4th instar	♀	♂	♀	♂
May 25	963	31				1	1		
27	199	69	2	1	1	1	1		2
30	63	32	31	7					1
June 2		28	107	4					
5		2	3	50	2				
9			1	4	10	1			
15			8	6				1	
24			2						
30									
July 7		1	3	1	2				
14			9	3	6				
20					4	1			1
27				2	1				
Aug 3				1	1				
10					1				
17			2		6	1			
25			1						
31				1					
Sept 8					2				
12									
Total	1225	163	169	80	36	7		5	

Sample size: 28.2 cc.

TABLE 11

Seasonal distribution of **D.grisea** in all stages at Morgan Arboretum pond, sites A and B, May 25 to September 12, 1964.

Date	Eggs	Larvae 1st instar	 2nd instar	 3rd instar	 4th instar	Pupae ♀	 ♂	Adults ♀	 ♂
May 25	1006	60							
27	295	87	2	1	1	3	2		
30	187	79	33	7		1	3	2	3
June 2	89	33	114	4					1
5		4	27	53	2				
9			2	14	11	1			
15			12	21	5			1	
24			5	3	6	2	1		
30					2	1	2	1	
July 7		1	3	1	2				
14		1	12	4	6				
20				1	15	1			1
27			3	7	9				
Aug 3			2	1	9				
10					1				
17		1	3		9	1			
25			2	1	1				
31			4	5	6				
Sept 8					2				
12			1						
Total	1577	264	235	123	92	18		10	

Sample size: 56.4 cc.

TABLE 12

Seasonal distribution of all chironomid species in all larval and pupal stages at Morgan Arboretum pond, May 25 to September 12, 1964.

Date	Site A	Site B	Sites A & B
May 25	85	40	125
27	16	66	82
30	47	25	72
June 2	48	32	80
5	243	19	262
9	200	28	228
15	105	24	129
24	72	*	72+
30	3	*	3+
July 6	26	11	37
14	49	43	93
21	*	44	44+
27	45	24	69
Aug 3	14	7	21
10	15	3	18
17	17	21	38
25	4	84	88
31	248	11	259
Sept 8	64	24	88
12	12	2	14
Total	1313	508	1821

Sample size: 28.2 cc. for sites A and B separately and 56.4 cc. for sites A and B combined.

* Counts missed

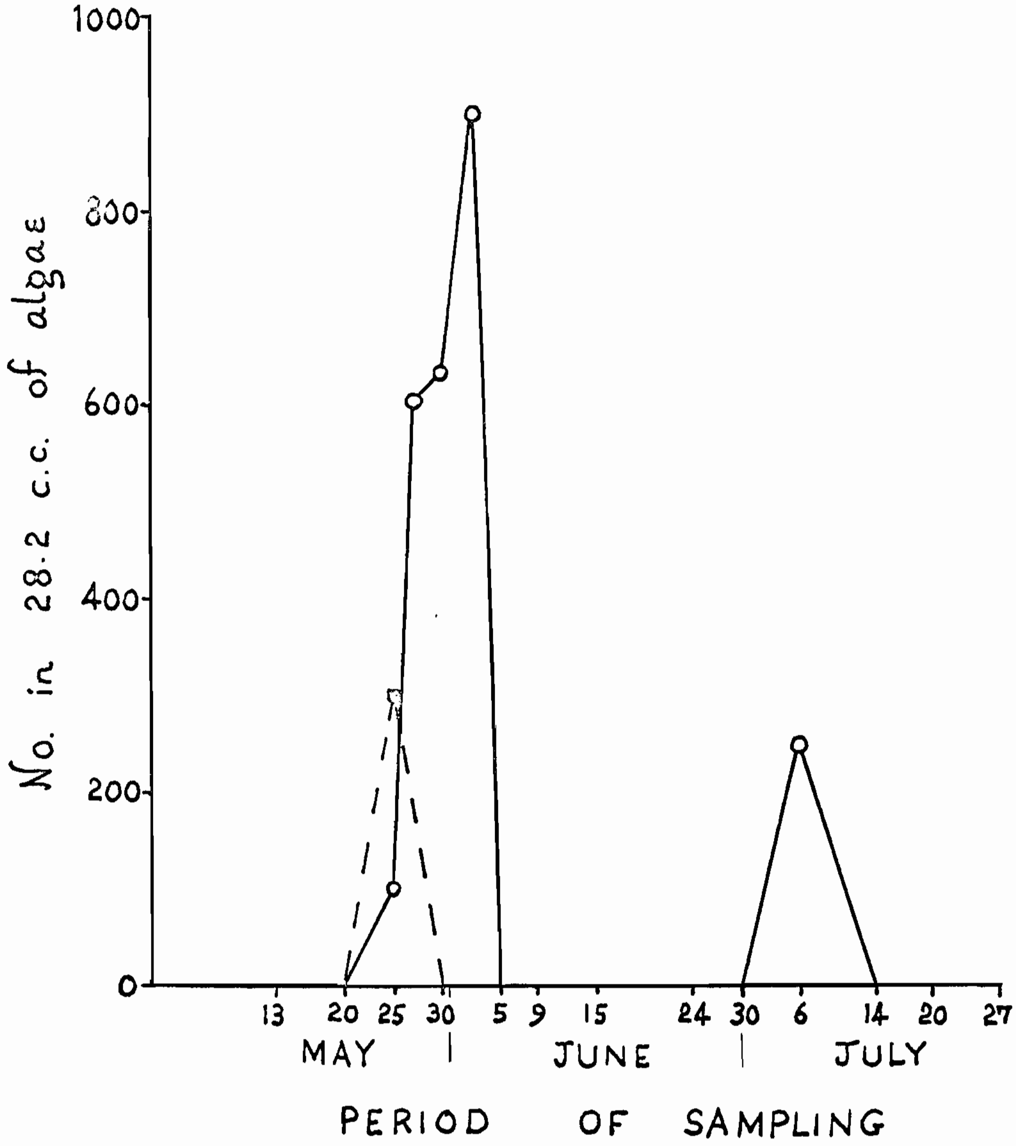
TABLE 13

Seasonal distribution of all larval stages of predator species (Palpomyia slossonae and Bezzia glabra) and all larval and pupal stages of prey species (all chironomid species)at Morgan Arboretum pond, during the sampling period, May 25 to September 12, 1964.

Date	Prey species	Predator species	No. prey attacked per predator
May 25	125	28	4.46
27	82	25	3.28
30	72	16	4.50
June 2	80	41	1.95
5	262	164	1.60
9	228	201	1.13
15	129	169	0.76
24	72	74	0.97
30	3	136	0.02
July 6	37	195	0.19
14	92	169	0.54
20	44	216	0.20
27	69	155	0.45
Aug 3	21	134	0.16
10	18	100	0.18
17	38	67	0.27
25	88	107	0.82
31	259	90	2.88
Sept 8	88	59	1.49
12	14	33	0.42

Sample size: 56.4 cc.

Fig. 43. Seasonal distribution of eggs of *P. slossonae*



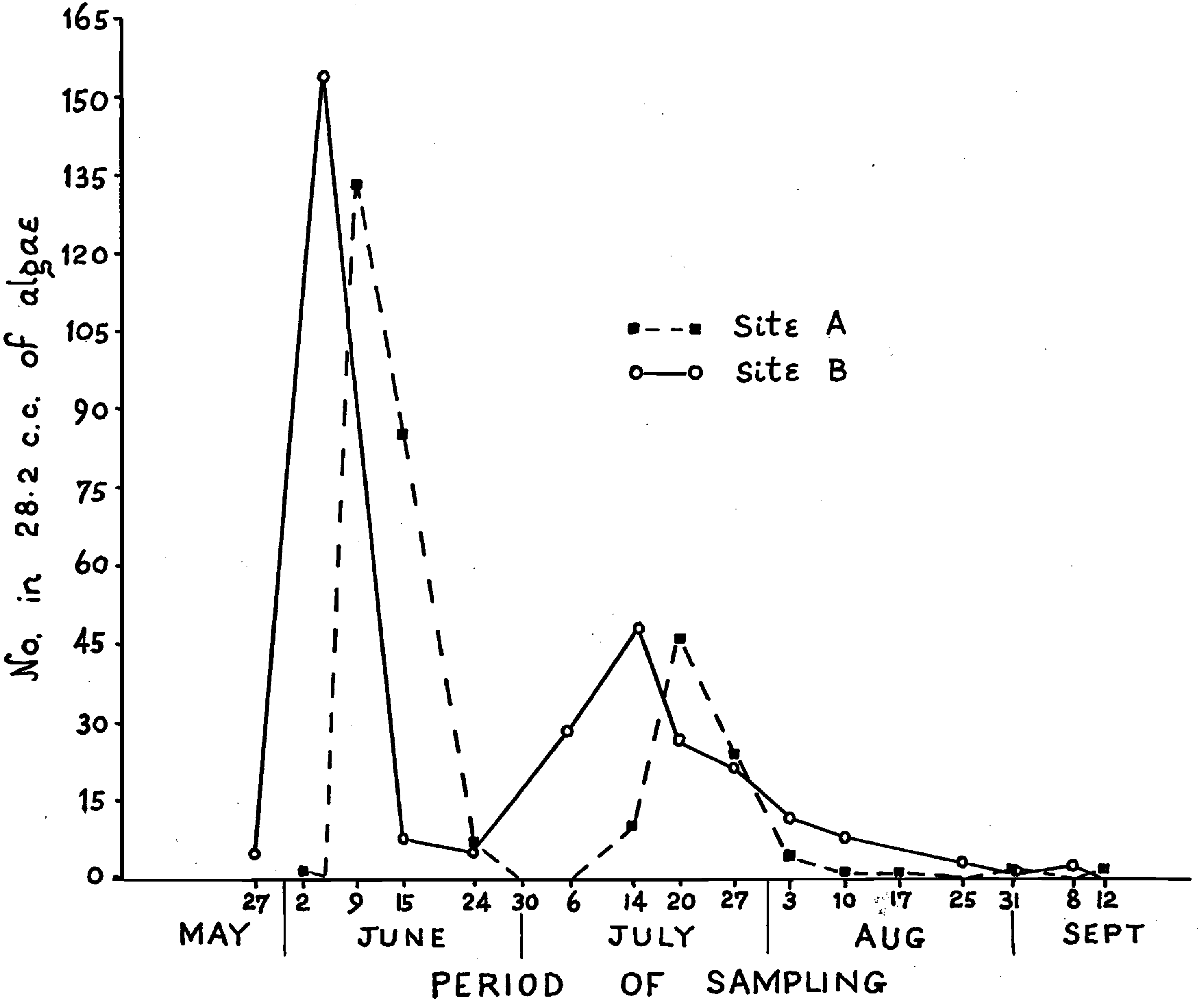
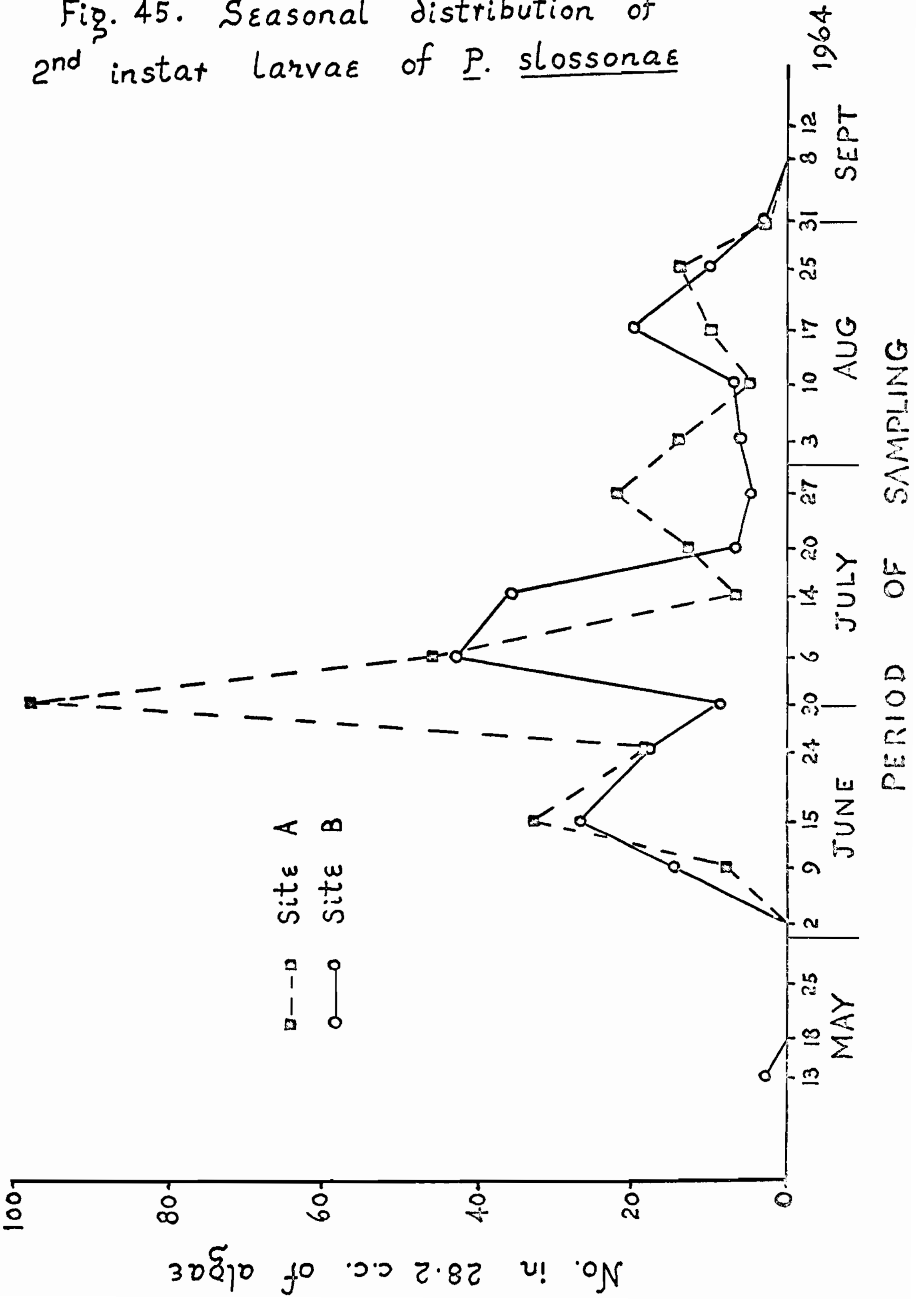


Fig. 44. Seasonal distribution of 1st instar larvae of *P. slossonae*

Fig. 45. Seasonal distribution of 2nd instat larvae of P. slossonae



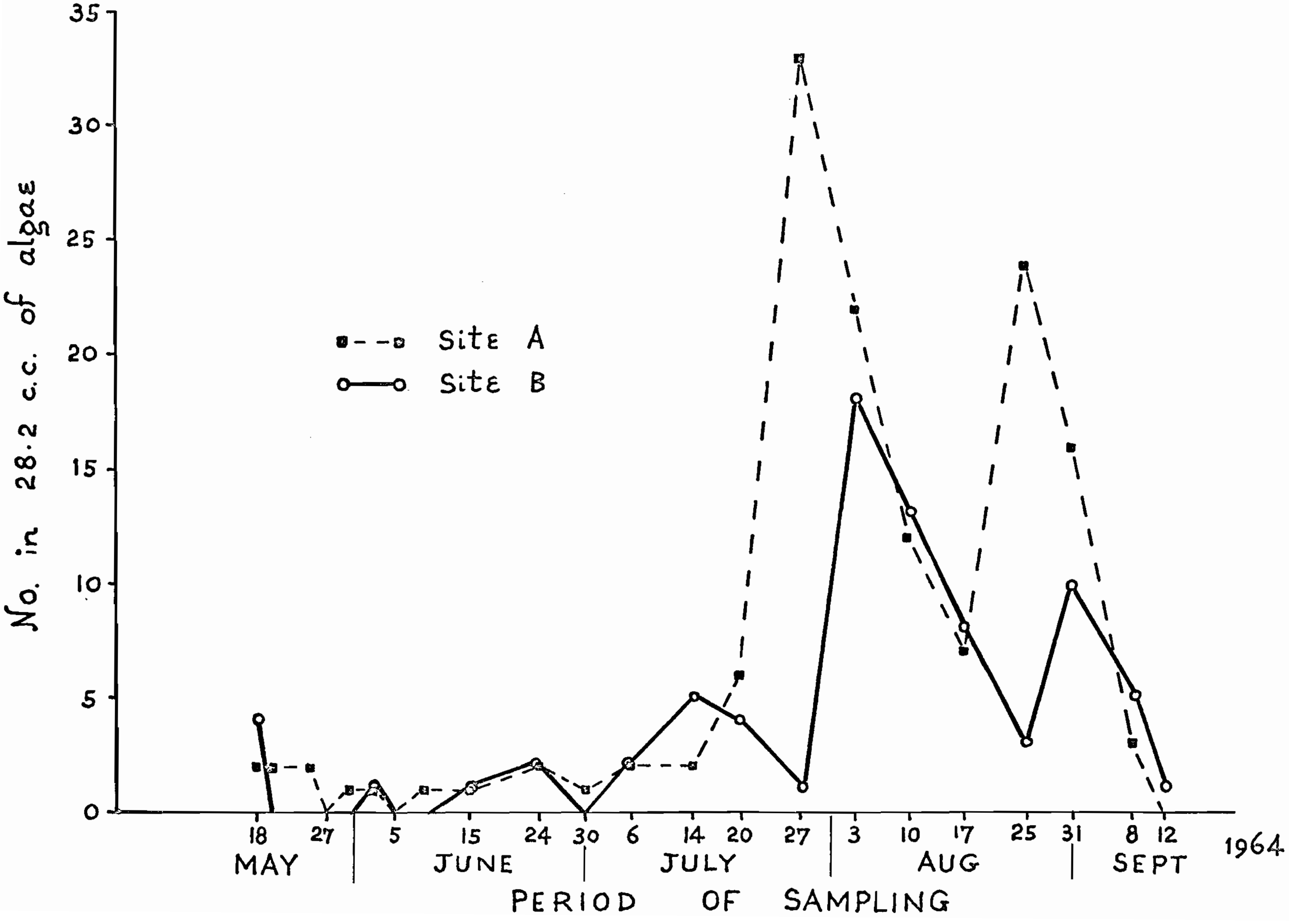


Fig. 46. Seasonal distribution of 3rd instar larvae of <u>P. slossonae</u>

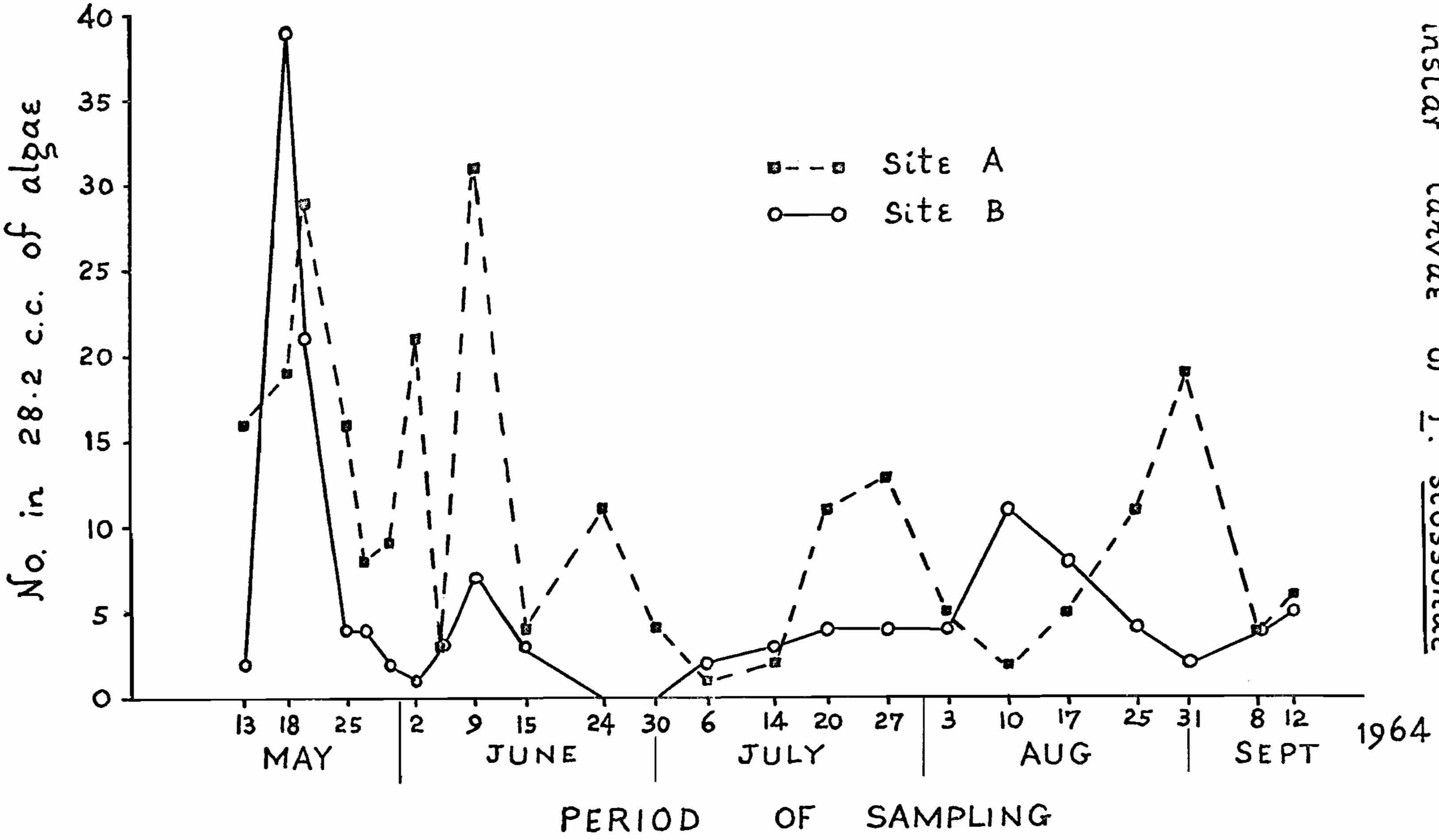


Fig. 47. Seasonal distribution of 4th instar larvae of P. slossonae

Fig. 48. Seasonal distribution of pupae of *P. slossonae*

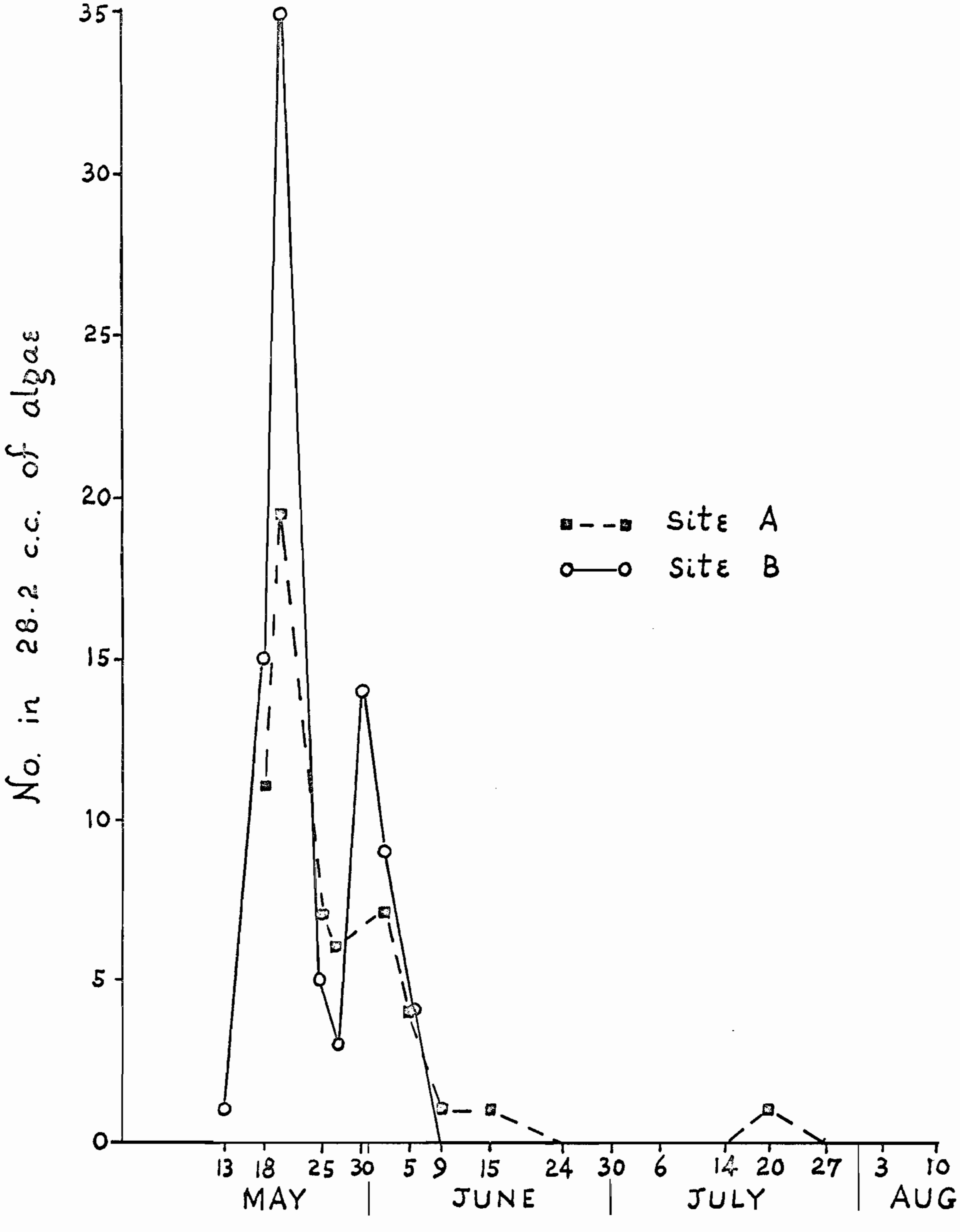
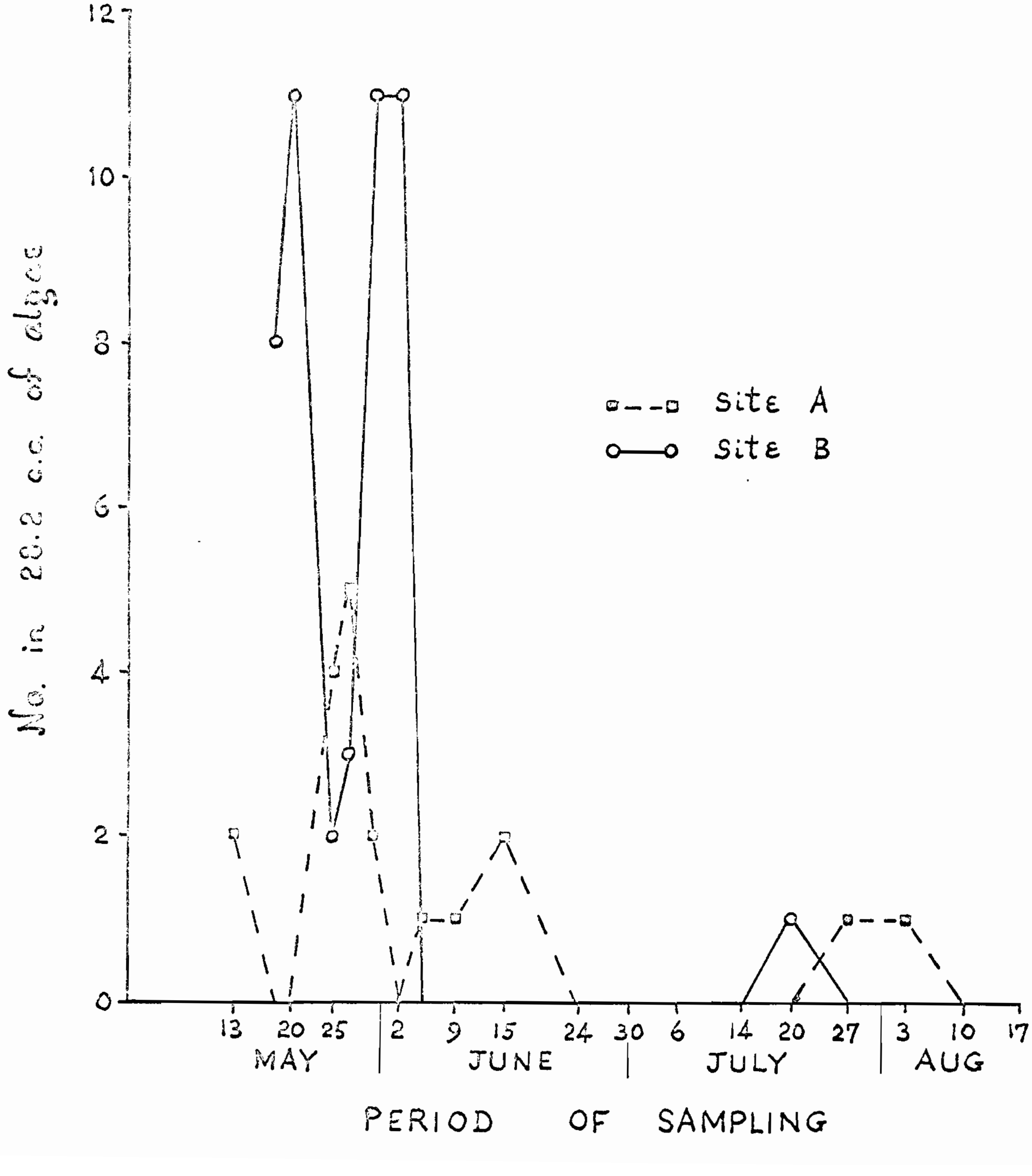


Fig. 49. Seasonal distribution of adults of *P. slossonae*



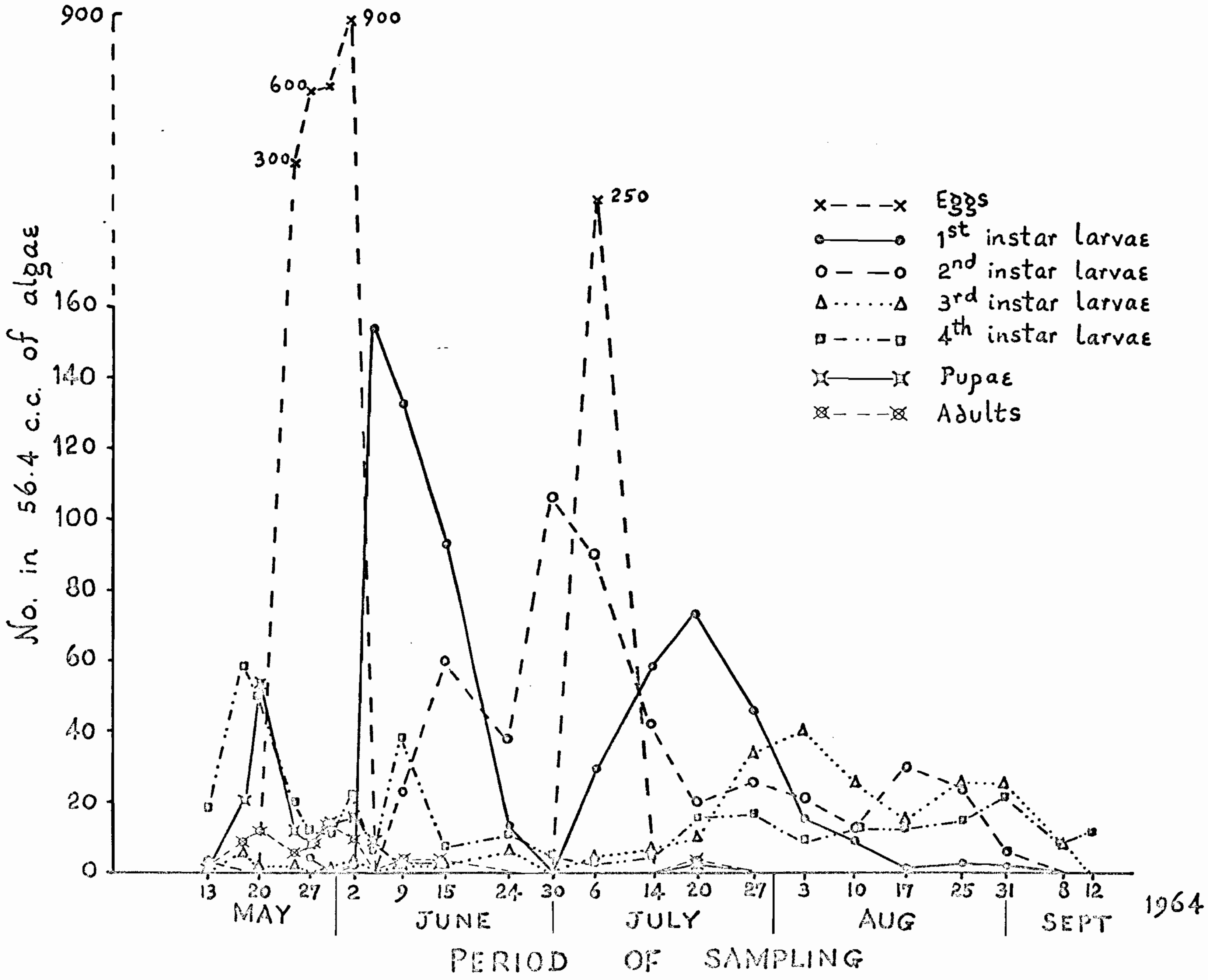


Fig. 50. Seasonal distribution of *Palpomyia slossonae* in sites A + B

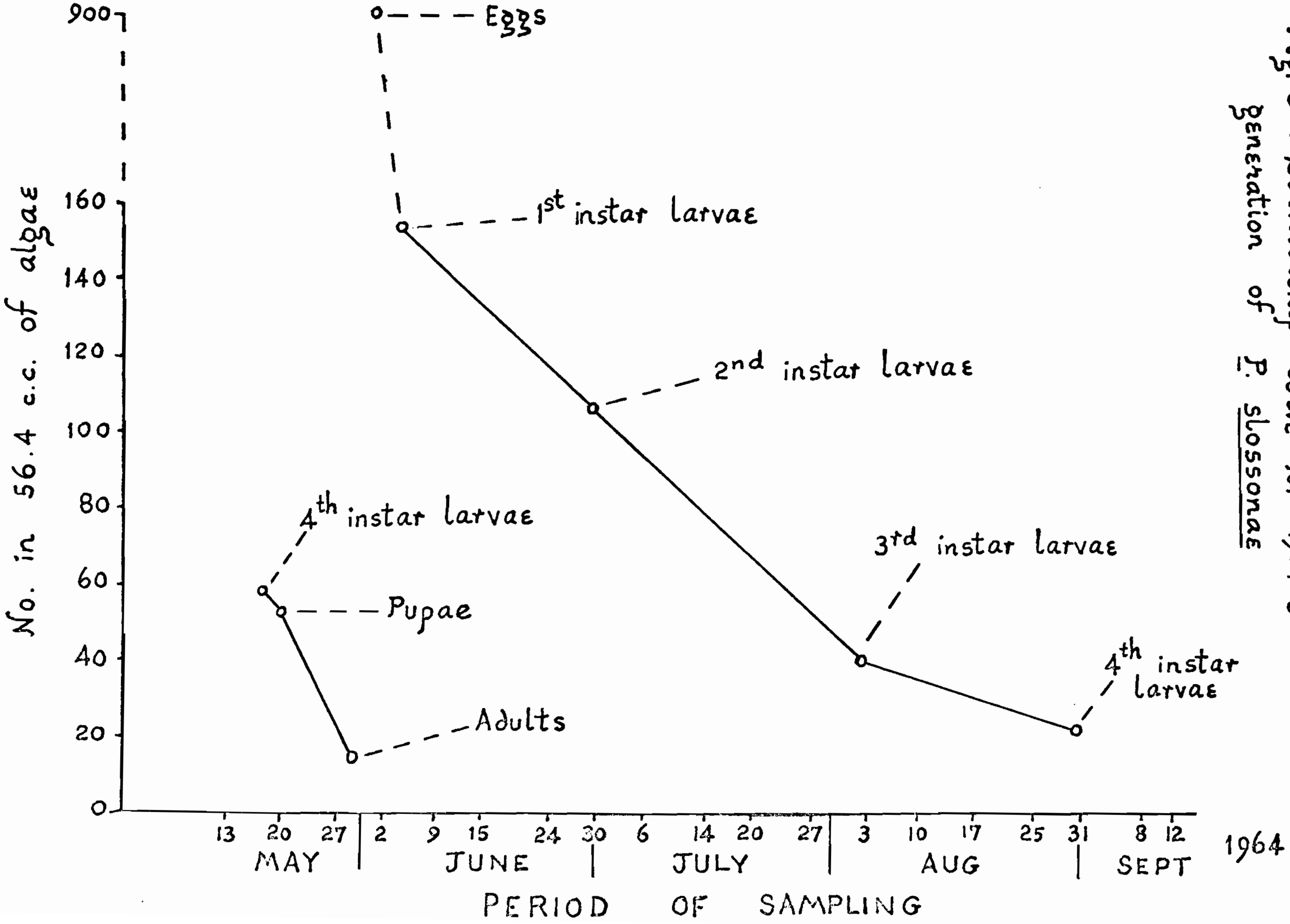
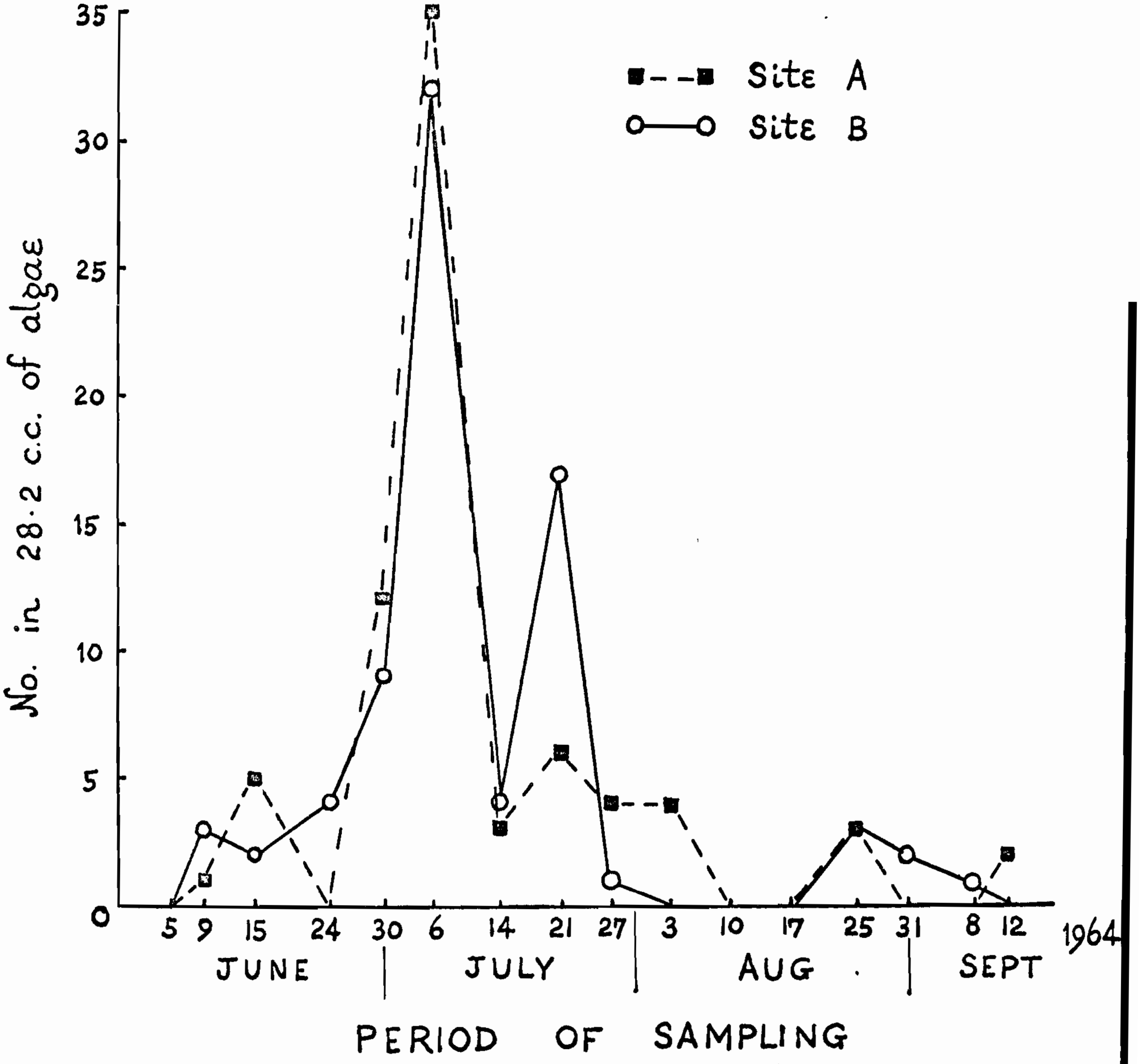


Fig. 51. Survivorship curve for 1964-5 generation of P. slossonae

Fig. 52. Seasonal distribution of 1st instar larvae of B. glabra



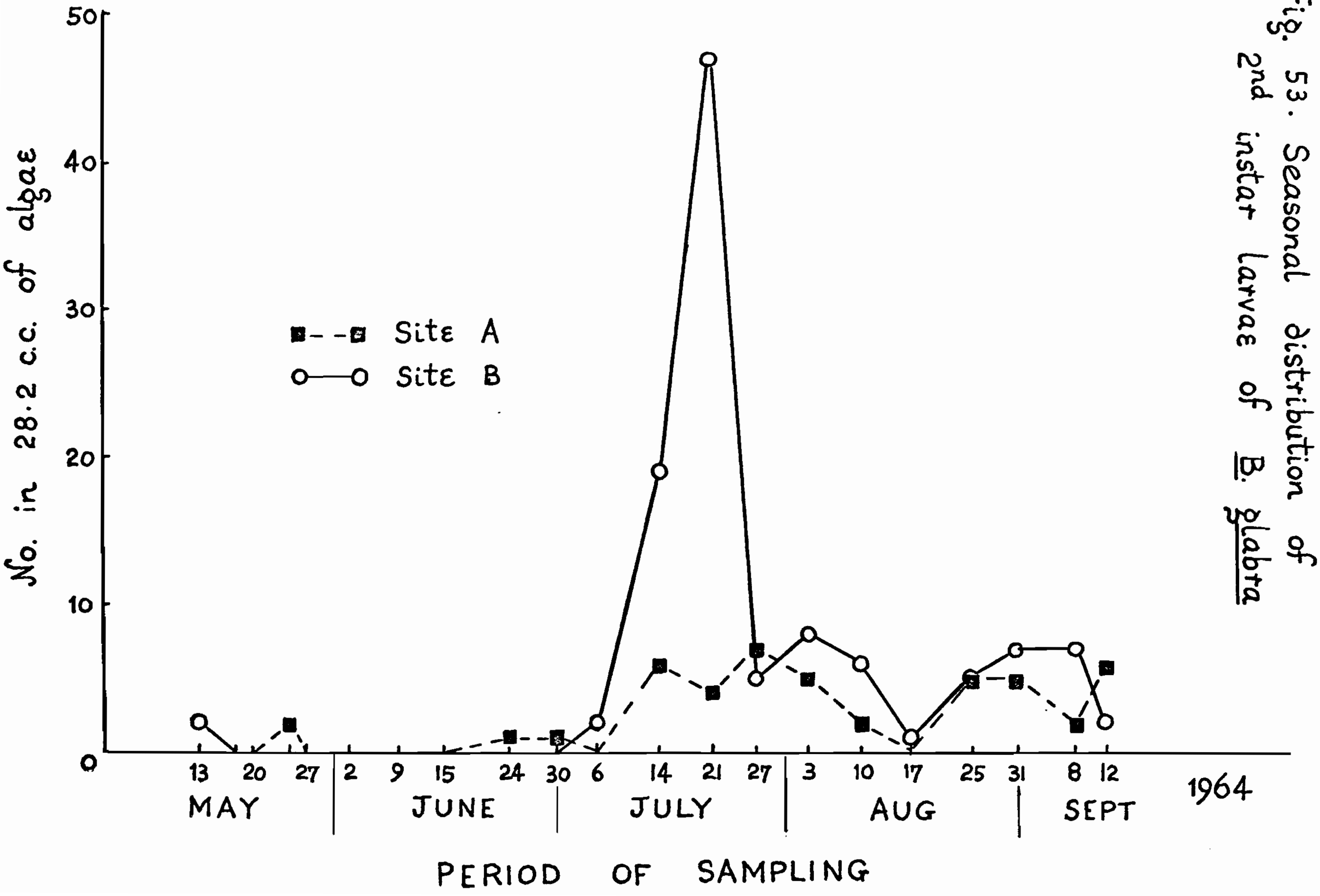


Fig. 53. Seasonal distribution of 2nd instar larvae of B. glabra

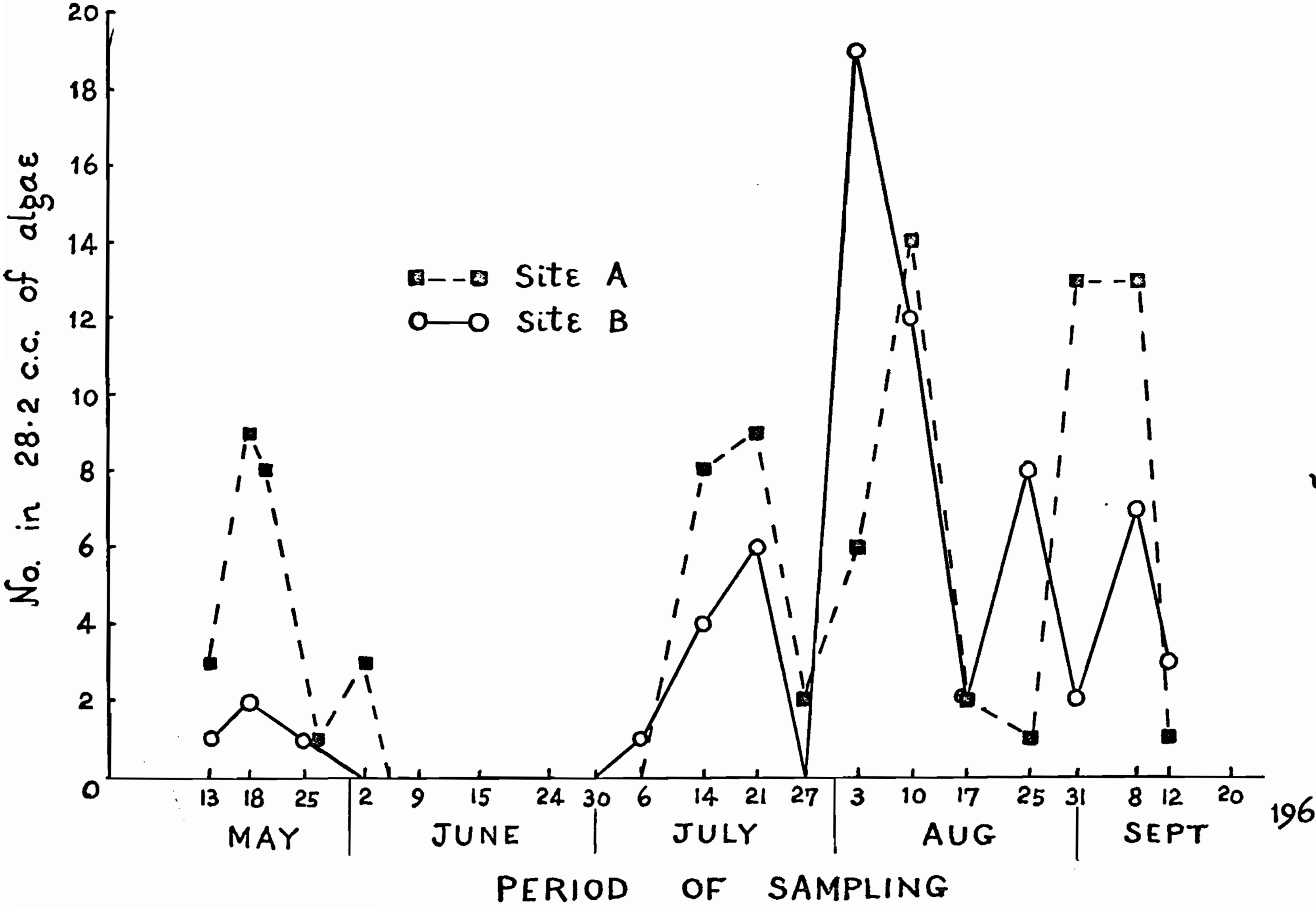


Fig. 54. Seasonal distribution of 3rd instar larvae of B. glabra

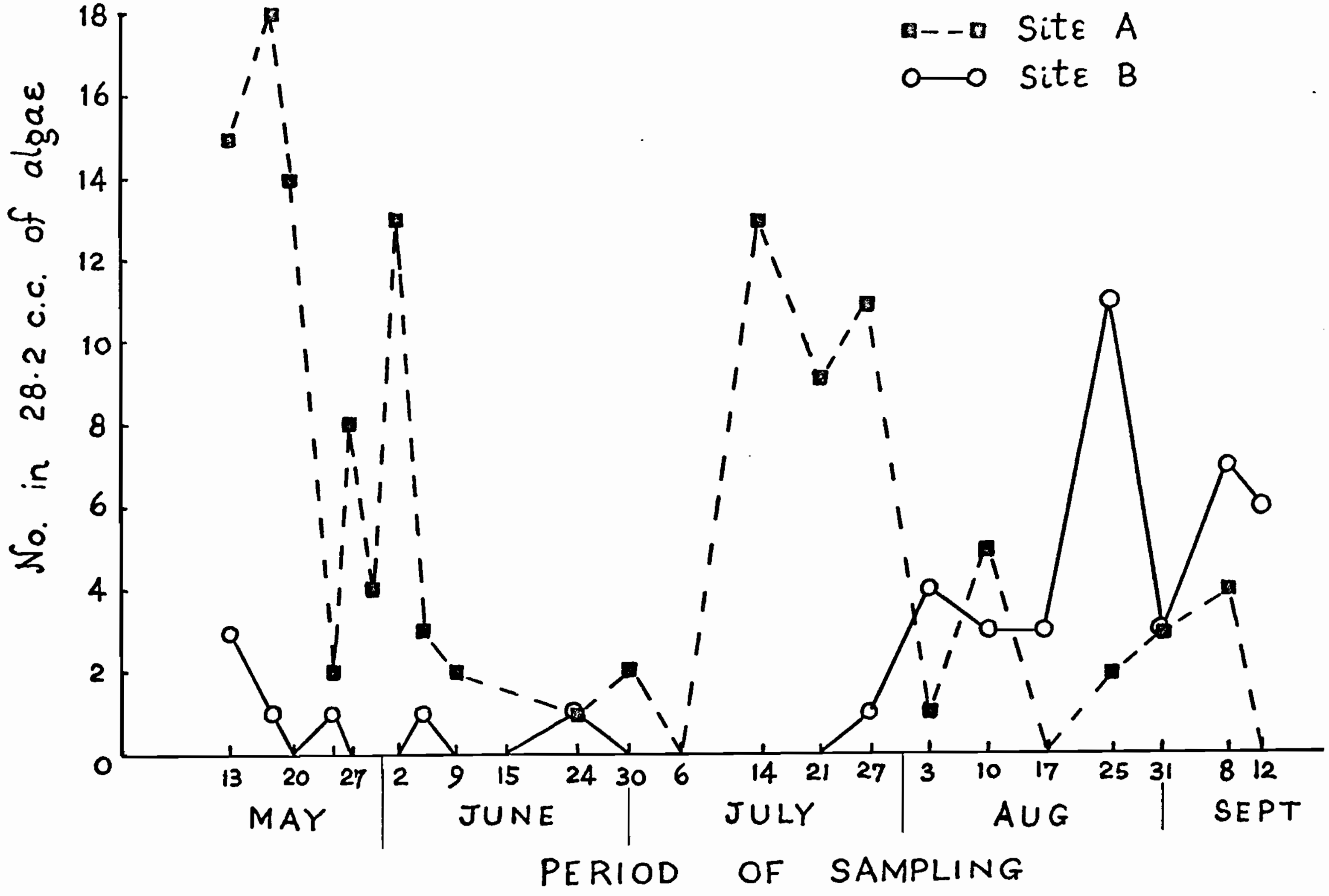


Fig. 55. Seasonal distribution of 4th instar larvae of B. glabra

Fig. 56. Seasonal distribution of pupae of B. glabra

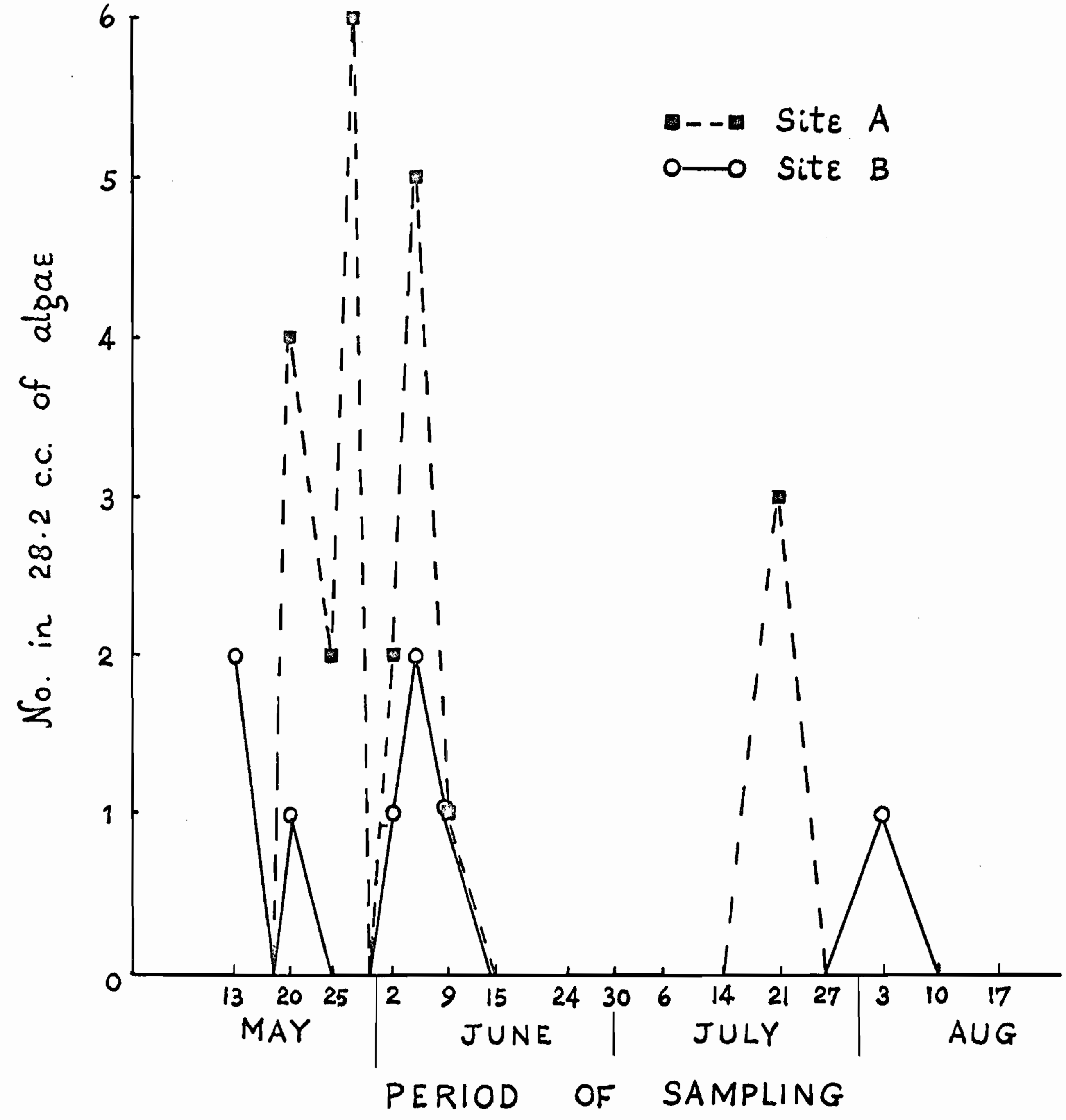
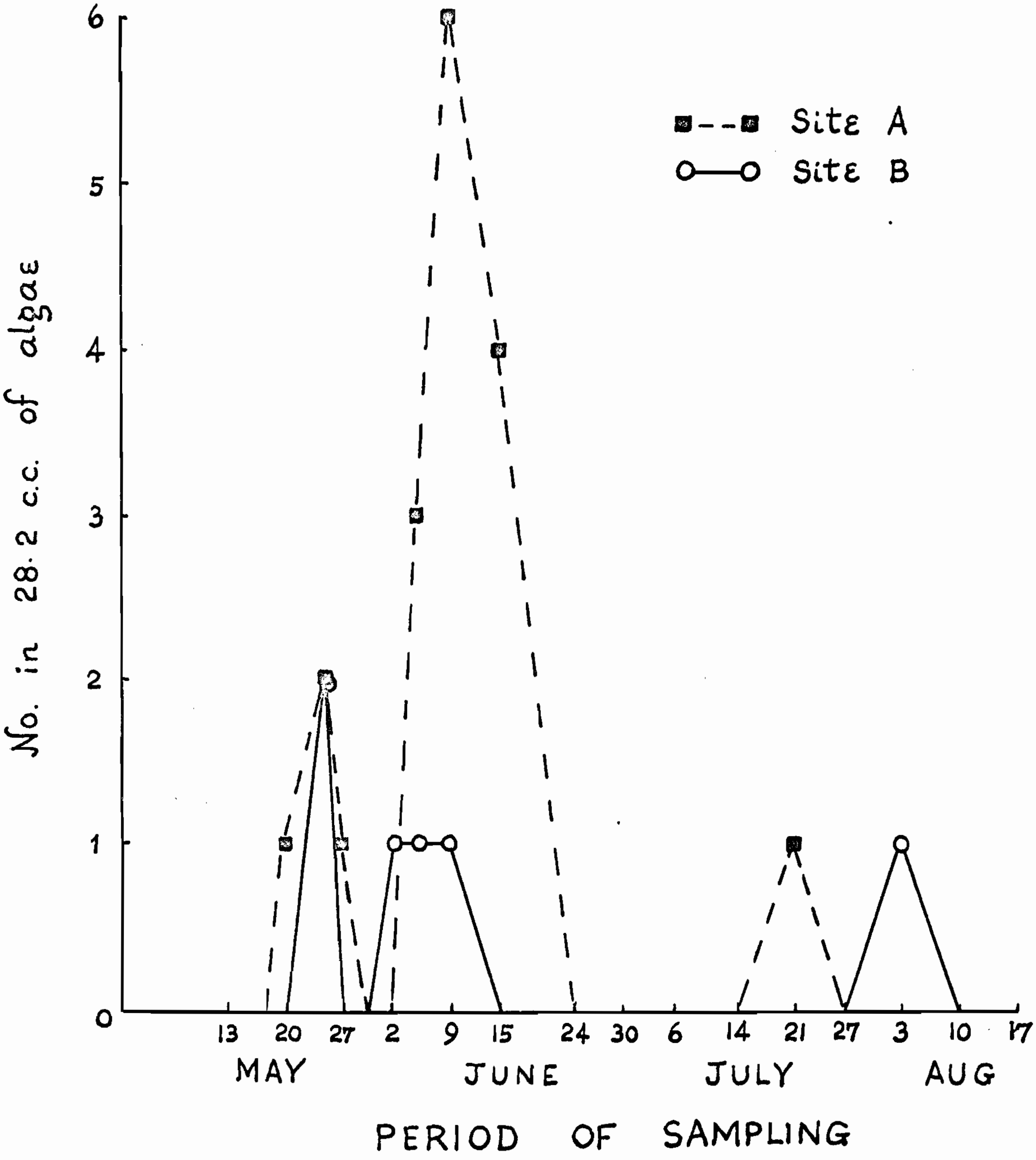


Fig. 57. Seasonal distribution of adults of B. glabra



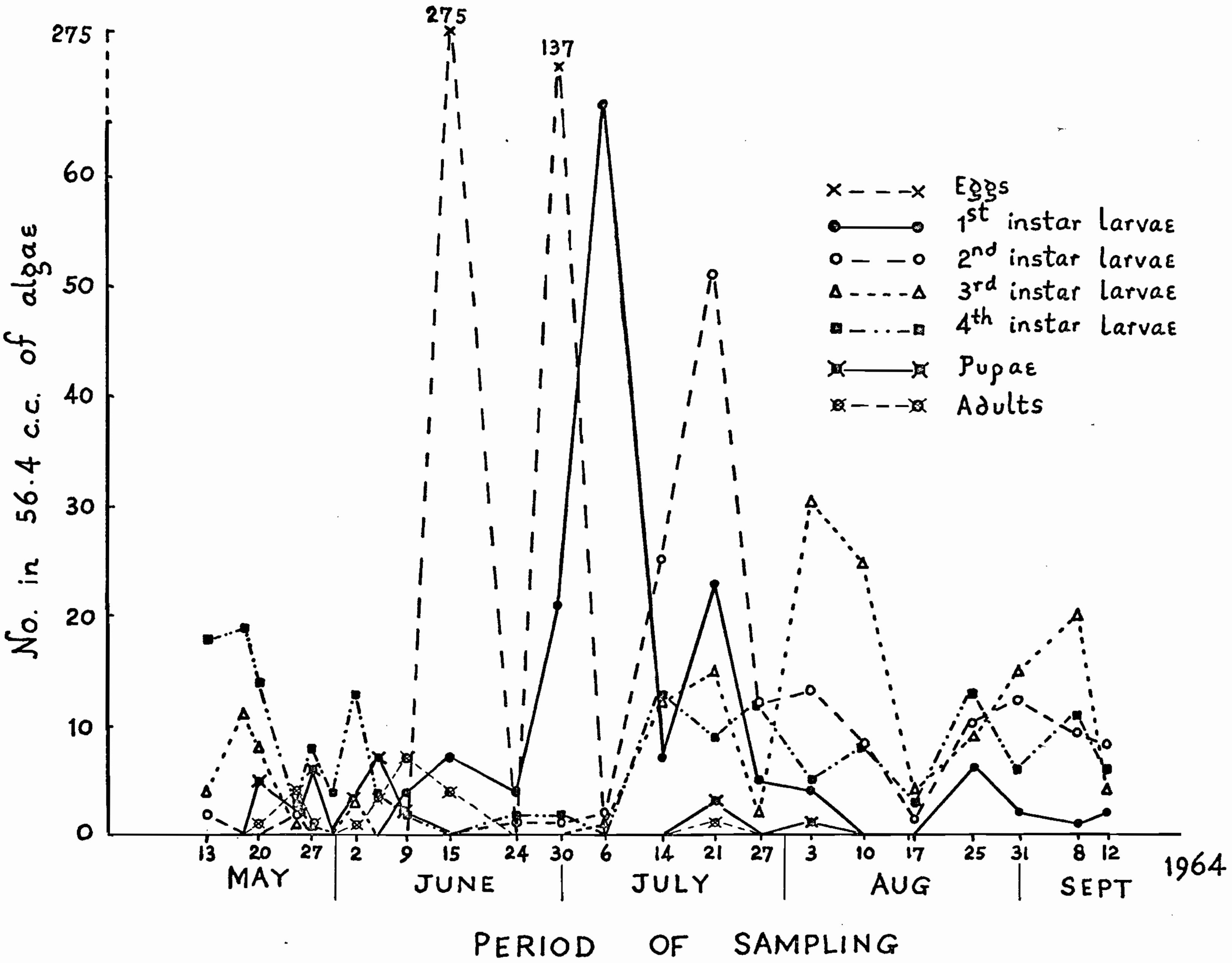


Fig. 58. Seasonal distribution of *Bezzia glabra* in sites A + B

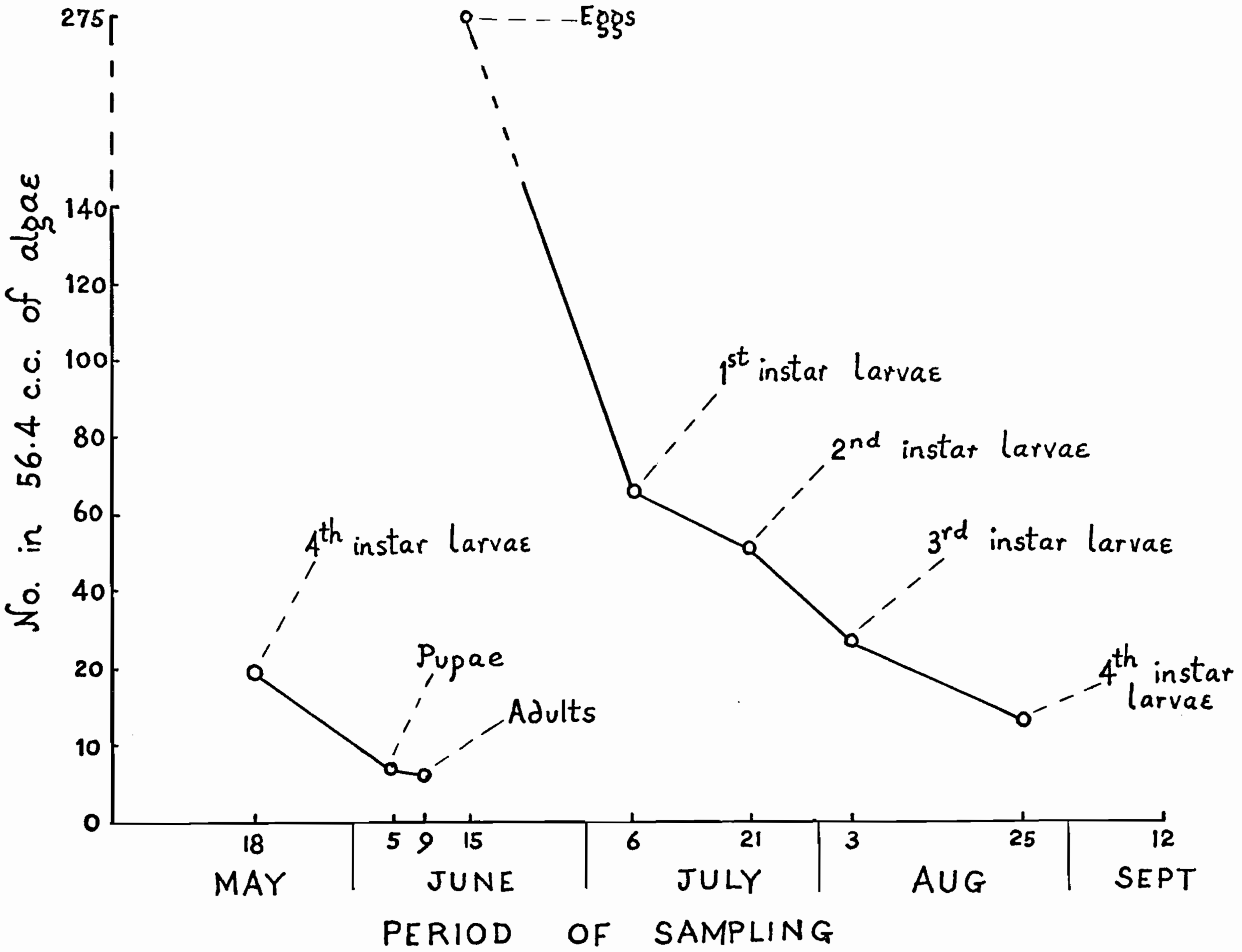


Fig. 59. Survivorship curve for 1964-5 generation of B. glabra

A. PALPOMYIA SLOSSONAE AND BEZZIA GLABRA

1. Eggs.

Eggs of P.slossonae were collected in two periods from May 25 to July 6 (Fig. 43) and of B.glabra only on June 15 and 30, 1964 (Table 8). Eggs of both species are laid and glued onto blanket algae, usually near a source of food --- chironomid eggs of about the same stage of development. Chironomid eggs were almost always laid on very young, light green algae since emerging first-instar larvae are only strong enough to feed on young algal filaments from which they make dwelling tubes.

Under the binocular microscope no morphological difference could be distinguished between eggs of P.slossonae and B.glabra and they were identified from the emerging larvae which are morphologically distinct.

Eggs were laid in batches, each roughly circular, resembling a cushion and consisting of about 300 eggs in P. slossonae and 200 in B. glabra. Each egg is cigar-shaped, light grey when newly laid, black after a day, about six times as long as wide and is surrounded by a gelatinous mass of jelly which separates it from its neighbours and binds it to them. Eggs hatched from two to seven days when reared at a temperature of 70°F. and a relative humidity of 50 per cent.

2. Larvae.

a). Food and feeding habits. - Both P. slossonae and B. glabra feed on the same types of food and show imperceptibly the same feeding habits. All species of organisms found in the pond with P.slossonae and B. glabra were carefully tested as possible food items but only chironomid larvae and D. grisea larvae were found to be captured and preyed upon and only in one instance was a crustacean attacked by a starved fourth-instar larva of P.slossonae. All species of chironomid larvae were found acceptable as food but certain species were preferred over others. These included a blood-red species collected from Ile Perrot River estuary taken from muddy water having a low oxygen content, and a local orange species, both unidentified. D.grisea larvae were found to be least preferred but when the predator larvae were starved for a few days, their degree of preference became less marked and they would feed somewhat indiscriminately on all species of chironomids and D.grisea.

It was observed that first instar larvae of P.slossonae and B. glabra generally attacked first-instar chironomid and D.grisea larvae but rarely instars larger than themselves. When second, third or fourth-instar chironomid larvae were attacked, vigourous struggling movements by the prey enable them to escape. In the laboratory, however, P.slossonae and B. glabra were fed large prey rendered defenseless by decapitation.

Second-instar larvae of both P.slossonae and B.glabra also show limited power of attack and fed on prey their own size, rarely on prey much larger than themselves.

Third-instar larvae are more powerful and can attack and overcome prey much larger than themselves while fourth-instar larvae are the most efficient and can usually overcome even the largest chironomid larvae without much difficulty.

Predators usually remain very still in the algal filaments, detecting movements of the prey at a distance of a few centimetres; sometimes showing no signs of awareness of the prey's presence until predator and prey come into contact. When the prey's presence is detected, the predator moves towards it, presumably by sight or smell, and when within a distance of two to three millimetres from it, strikes with extended mandibles which hook on the body of the prey like a fishing hook, thus securing a firm hold. The attack is immediately followed by vigorous struggling movements of the prey to escape. This may last a good three minutes or more but usually much less. The predator usually overcomes the prey by pulling it into a thick mass of algal filaments, moving backwards as it pulls the prey. Being thus surrounded by algal filaments the prey is prevented from struggling too vigorously. Soon after securing a firm hold on the prey the predator begins to suck the body fluids out through the puncture made by the mandibles. Peristaltic movements of the gut contents of the predator can be seen as feeding proceeds and prey hemolymph and body contents from the prey flow into the predator's alimentary canal. Coincident with this action is the pouring of salivary juices into the prey body. The predator's pharynges move actively as it feeds. Feeding stops when the predator is satiated, i.e. when the whole gut can be seen to be filled with the prey's hemolymph. When the prey is small, as it often happens, the predator will feed on another prey until it is satiated. In every case only the body fluids of the prey, sometimes a little of the gut contents, are consumed. When the predator is satiated, the empty skin of the prey, sometimes the skin plus body fluids, as the case may be, is abandoned. If a hungry predator happens to come by a half finished prey, the latter will be seized and fed upon. Sometimes two or more predators can be observed feeding on the same prey.

When a prey is attacked in open water, the predator grasps it with its mandibles, then straightens itself out perpendicular to the struggling prey. As the prey rotates and gyrates through the water, the predator remains at right angles to the prey or sometimes coils round the prey, paralysing it with a secretion which it pours into the prey body.

Pupae of chironomids and D. grisea are also preyed upon but appear to be less preferred than larvae. This is surprising since these stages, because of their limited mobility, are easily overcome. This lack of preference may be due to the thicker exocuticle of the pupae, and lack of mobility. For the predator, movement on the part of the prey acts as a stimulus to feeding.

P. slossonae and B. glabra larvae are cannibalistic as well as predatory and were observed to attack all stages of larvae of their own species. In no instance was a small larva found to prey on a much larger one. Prepupae which do not feed, and are generally more sluggish than the actively feeding instars were particularly vulnerable to predation by individuals of the same species. Larvae about to moult, which like prepupae are sluggish and non-feeding, are also vulnerable to predation. Similar cannibalistic behaviour has also been observed by Thomsen (1937) for Palpomyia pruinescens Thomsen (synonym of slossonae?).

When the larvae are about to moult they stop feeding and soon their eye pigments move to the posterior region of the head capsule. After moulting the eye pigments are located in the normal position i.e. anterior third part of the head. By observing in the same individual the movements of the eye pigments in the head capsule it is very easy to count the number of instars in the life cycle. The premoulting (posterior) position of the eyes lasts from one to three days. The eyes at the posterior region of the head capsule are in all probability those of the succeeding instar whose head capsule lies in the posterior region of the old. Even in the fourth-instars the eye pigments are withdrawn to the posterior region just prior to pupation.

b). Locomotion.- Both P.slossonae and B. glabra show precisely the same kinds of movements. Both are capable of forward and backward movements in open water as well as in algae. Normal swimming movements in water is a lashing movement from side to side along a straight axis. Thus when swimming, they resemble tiny snakes moving through water. In their normal algal filament substratum, they are extremely agile and quick in winding and twisting through the filaments, both forwards and backwards. When disturbed with a dissecting needle they move away from the source of disturbance either forwards or backwards, depending on which half of the animal is nearer the needle, or point of disturbance. If the anterior half is nearer the point of disturbance the animal will back away and if the posterior half is nearer, the animal will proceed forward. When, however, the point of disturbance or stimulus is that made by a prey, the animal will always respond by moving towards the prey.

c). First Instar.- First-instar larvae of P.slossonae were collected from May 27 to September 12, 1964, in greatest numbers on June 5 (Table 5, Fig. 44). Those of B.glabra were collected on June 9 to September 12 and were in greatest numbers on July 6 (Table 8, Fig.52). As with their eggs, the larvae of the two species are found in young, light green algae. The two species can be separated easily by the shape of the head capsule and by the difference in colour of the body. The head capsule of P.slossonae is wider than that of B.glabra and the body colour of the former is brown while that of the latter is green like that of the blanket algae. The body width of P.slossonae is also generally stouter than that of B. glabra.

After emergence first-instar larvae of both species remain for about a day around and within the jelly of their egg masses. On the second and subsequent days after hatching they will actively search for food and will attack chironomid larvae of any stage.

Twenty first-instar larvae of P.slossonae, reared successfully in the laboratory on larvae of D. grisea and on larvae of different species of chironomids, took from 10 to 19 days or a mean of 14.25 days to complete their larval development. One first-instar larva of B. glabra successfully reared under similar conditions took eight days to complete its development.

From hatching to moulting, body length of P. slossonae ranges from 1.20 to 2.63 mm. for 26 individuals measured and that of B. glabra, from 1.35 to 2.18 mm. for five specimens measured. The lengths and widths of their head capsules range from 0.62 to 0.66 mm. and 0.26 to o.28 mm. for P. slossonae and respectively 0.59 to 0.60 mm. and 0.20 to 0.21 mm. for B. glabra.

d). - Second instar.- Second-instar larvae of P. slossonae were collected on May 13 and from June 9 to August 31, 1964, and were obtained in greatest numbers on June 30 (Table 5, Fig. 50). B.glabra second-instar larvae were collected on May 13 and 25 and from June 24 to September 12, 1964, during which the peak incidence occurred on July 21 (Table 8, Fig. 53).

Second-instar larvae of both species were almost always found in very young green algae where first- and second-instar larvae of chironomids occurred in greatest abundance.

The duration of the second stadium was successfully obtained from laboratory rearings for 19 and 6 individuals respectively of P.slossonae and B.glabra. These took respectively 10 to 22 days with a mean of 14.26 days and 8 to 23 days with a mean of 14.3 days.

The range of body length from moult to moult is 2.40 - 4.11 mm. for 13 individuals in P. slossonae and 2.10 - 4.19 mm. for 24 individuals in B. glabra. Head capsule lengths and widths range respectively from 0.87 - 0.98 mm. and 0.27 - 0.30 mm. for 24 individuals of B. glabra and 0.89 - 0.96 mm. and 0.33 - 0.36 mm. for 13 individuals of P. slossonae.

e). Third instar. - Larvae of P. slossonae were collected from May 18 to September 12, 1964, and these occurred in greatest numbers on August 3 (Table 5, Fig. 50). Those of B. glabra were also collected during this period but none were collected between June 5 and June 30(Table 8, Fig. 58).

Unlike first- and second-instar larvae, third-instar larvae were not found associated with any particular type of green algae but were more or less uniformly distributed in rather clean and thick algae. Wherever chironomid larvae were found in fair numbers third-instar larvae were also found in large numbers.

The duration of this stadium in the laboratory, for 16 individuals of P. slossonae from beginning of moult to the next took 7 - 58 days, with a mean of 35.19 days and for five individuals of B. glabra 16 - 35 days, with a mean of 24.4 days.

The length of 21 third-instar specimens of P. slossonae measured during the period "beginning of second moult to the end of the stage" range from 3.30 mm. to 7.46 mm. and that of 48 individuals of B. glabra from 3.27 mm. to 6.68 mm. The lengths and widths of the head capsules for B. glabra range respectively from 1.29 mm. to 1.49 mm. and 0.35 mm. to 0.45 mm., and for P. slossonae 1.28 to 1.41 mm. and 0.45 mm. to 0.46 mm.

f). Fourth instar.- Larvae of both P. slossonae and B. glabra were collected throughout the sampling period, May 13 - September 12, 1964, and in greatest numbers, on May 18 (Table 5, Fig. 50; Table 8, Fig. 58). Fourth-instar larvae were usually found in large numbers in young and old algae where chironomid larvae were present, but not in excessively muddy areas of the pond.

The duration of this stage was successfully determined under laboratory conditions for seven individuals of B. glabra which took 11 - 19 days, with a mean of 15.7 days. These larvae, collected as third-instar larvae in the last week in May, became pupae by about the second week of June. The duration of the stadium for fourth-instar larvae of P. slossonae, on the other hand, could not be determined. Third-instar larvae which became fourth instars on or around July 23 and August 6 did not pupate but overwintered in this stage. Fourth-instar larvae collected in early May pupated and became adults by about the end of May. It appears therefore that for B. glabra the fourth instar stage lasts from the end of July or beginning of August to the last week of May, i.e. about nine months.

3. Pupae.

Pupae of P. slossonae were collected from May 13 to June 15 and again on July 20, the greatest numbers occurring on May 20 (Table 5, Fig. 50). Presumably pupation of the overwintering fourth-instar larvae took place much earlier. Pupae of B. glabra were also collected from the beginning of the sampling period to June 9 and again on July 21 and August 3 when only three females and one male respectively were collected. Peak numbers occurred on June 5 (Table 8, Fig. 58).

Sexual dimorphism in the pupae of both species is evident, the female in both species being usually much larger than the male. The lengths and widths of 22 male pupae of P. slossonae are respectively 3.65 - 4.50 mm. and 0.72 - 0.86 mm. and those of 45 female pupae 4.14 - 5.85 mm. and 0.87 - 1.20 mm. The lengths and widths of 30 male B. glabra pupae are respectively 3.18 - 3.84 mm. and 0.50 - 0.66 mm. and those of 37 female pupae 3.60 - 4.50 mm. and 0.60 - 0.77 mm.

Both P. slossonae and B. glabra larvae pupate in the algae, usually near the upper surface and remain attached to this substrate by their terminal processes for some time after pupation but with their respiratory horns always open at the water surface. The colour of P. slossonae pupae just after pupation is light brown and in B. glabra light green. After one day P. slossonae become dark brown to almost black and B. glabra pupae light brown. They then work their way to the water's edge or are carried there by water currents as observed by Thomsen (1937). A few however remain attached to the algae until adult emergence.

Pupae of both species are capable of moving the abdomen and can wriggle quite vigorously when disturbed.

Pupal duration is short in both species, averaging 2.3 days for 23 individuals in B. glabra and 3.9 days for 30 individuals of P. slossonae.

4. Adults.

Adult emergence was counted from the number of empty pupal cases. These were usually collected floating on the water surface.

As pointed out by Corbet (1964) adult emergence determined this way by actual counts of pupal exuviae provide comprehensive counts, and the accuracy of this comprehensive method depends on the insect's size and emergence habits and on the site where it is being studied. Of the three methods of determining emergence (i.e. counting adult numbers) namely, comprehensive, indirect and representative, the first is presumably the most accurate.

Empty pupal cases were collected from May 13 to June 15, 1964, and again from July 20 to August 3, for *P. slossonae* where greatest numbers occurred on May 30 (Table 5, Fig. 50). Those of *B. glabra* were collected during the same periods (Table 8, Fig. 58), greatest numbers occurring on June 9.

Sexual dimorphism also exists in both *P. slossonae* and *B. glabra* adults, the males usually being much smaller than the females. Their length ranges from 3.32 - 4.77 mm. for 46 females and 2.25 - 3.45 mm. for 44 males of *P. slossonae* and 2.63 - 3.39 mm. for 25 females and 2.12 - 3.03 mm. for 26 males of *B. glabra*.

The longevity of adults in nature is not known but from laboratory rearings on 10 per cent sucrose solution (Chan and Saunders, 1965), adults did not live more than a week, usually dying within two or three days following emergence. Moreover, unlike most species of *Forcipomyia* s. str. and *Lasiohelea* s. str., the females cannot mature their eggs on 10 per cent sucrose solution, thus indicating that these forms require a blood meal for growth and maturation of occytes. That this is very likely is confirmed from examination of their mouthparts. Females of both species have very well-developed mouthparts, the mandibles bearing large, well-developed teeth. Like most of the higher forms, they probably catch in flight other insects of about their own size such as chironomids and small mayflies, and suck the body fluids, killing their prey in the process (Edwards, 1923). Males and females of both species, however, will feed readily on sucrose solution.

Mating does not take place in confinement (3" x 1" tubes) and adults of both species probably require a swarm for this purpose.

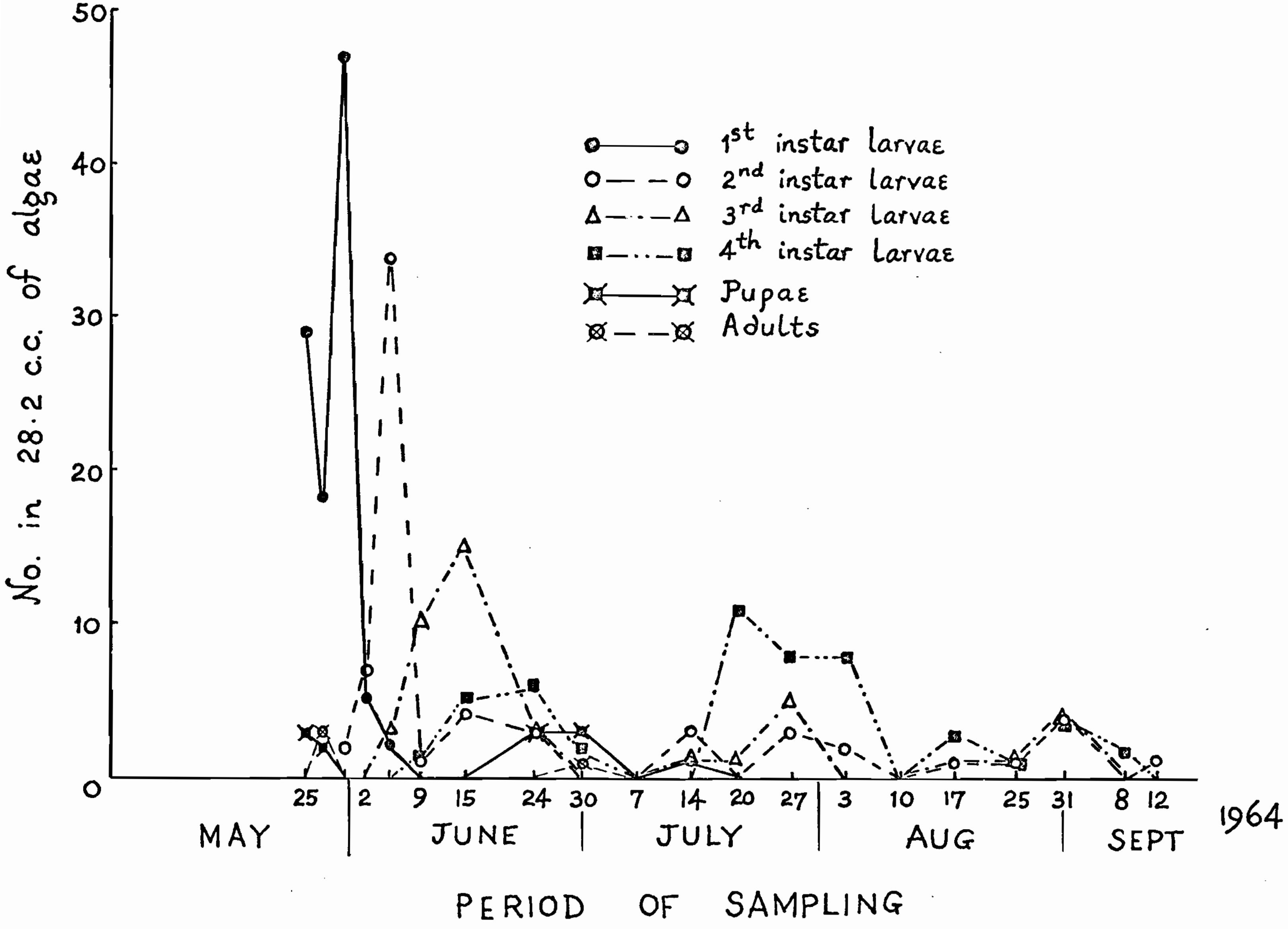


Fig. 60. Seasonal distribution of *Dasyhelea grisea* in site A

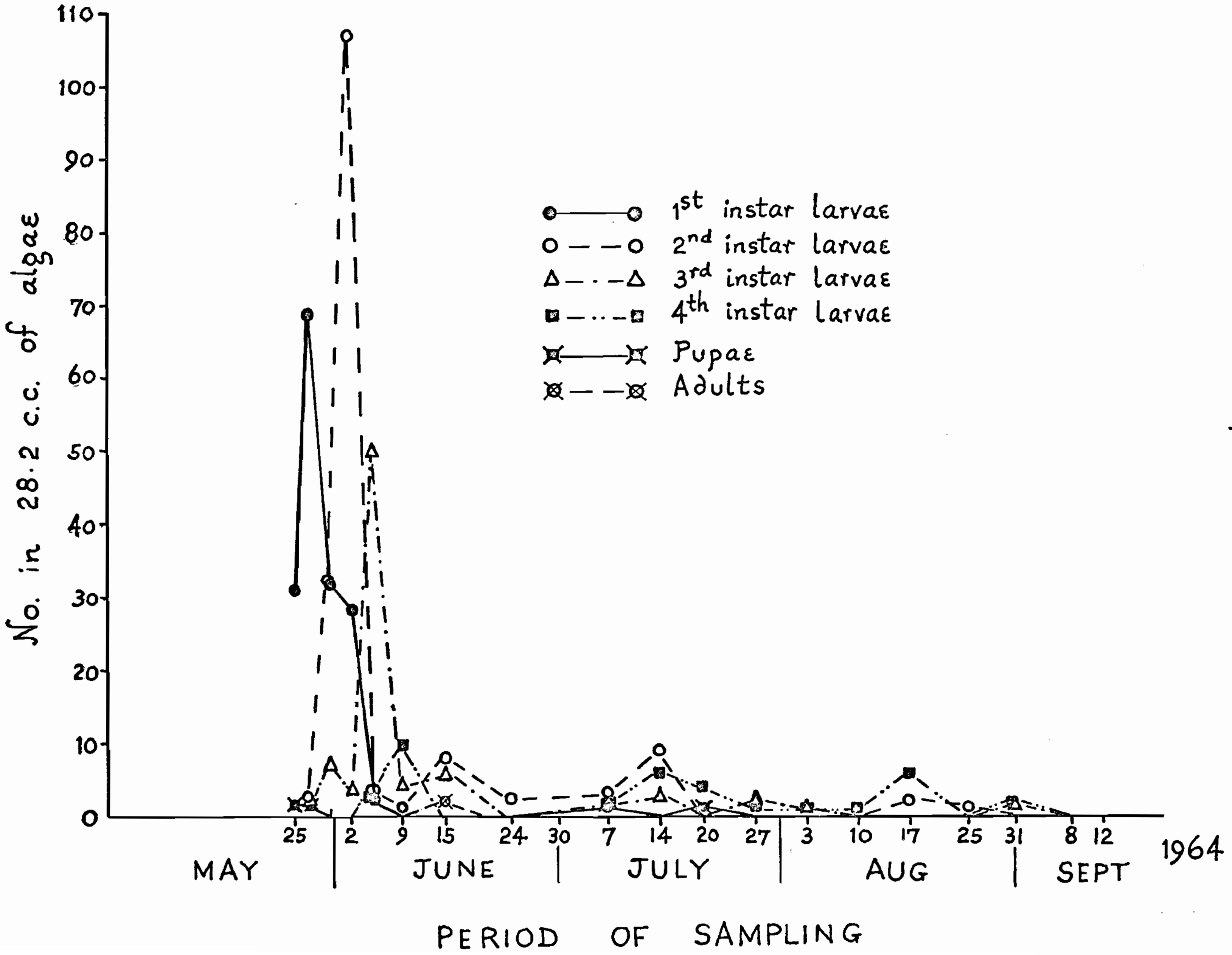


Fig. 61. Seasonal distribution of *Dasyhelea grisea* in site B

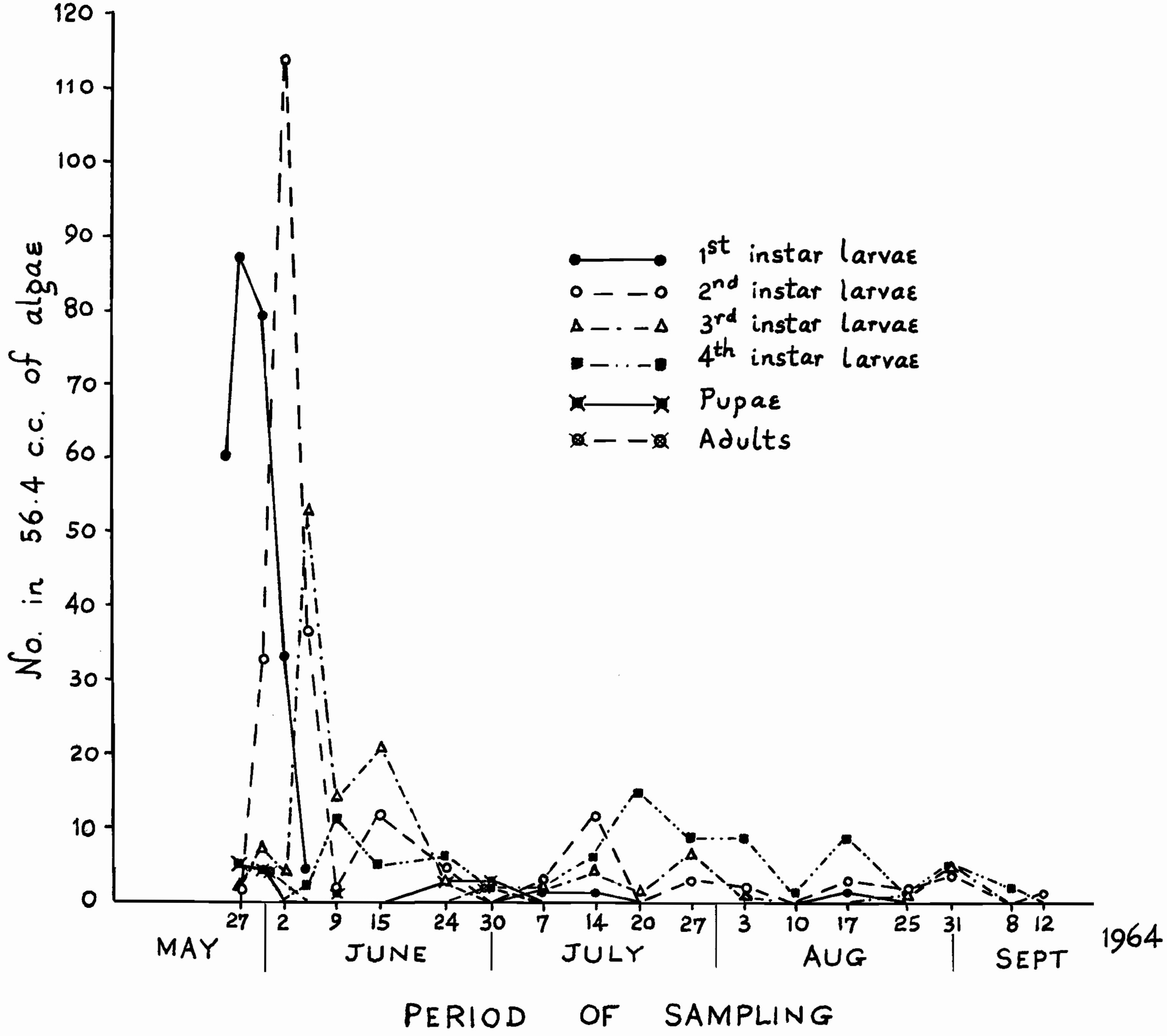


Fig. 62. Seasonal distribution of *Dasyhelea grisea* in sites A + B

B. DASYHELEA GRISEA

1. Eggs.

Eggs were collected from May 25 to June 2, with the greatest numbers occurring on May 25 (Table 11). They were laid on brownish-green, freshly dead blanket algae, surrounded by a thin film of dead tissue and often a collection of debris. Twenty-two egg masses were obtained. Each mass has a rather flattened appearance, the eggs being held together by a gelatinous layer. The number of eggs per mass range from 4 - 167, or an average of 72. Thomsen's (1937) record of 15 - 80 eggs per batch falls within this range.

Newly laid eggs are light brown but after a day become dark-brown to black. Individual eggs are long and horseshoe-shaped in structure, and are separated from each other by a gelatinous covering about the thickness of each egg.

The eggs hatched from one to four days after they were brought to the laboratory, thus indicating that the duration of the egg stage is at least four days at a temperature of 70°F. and a relative humidity of 50 per cent.

2. Larvae.

a). <u>Food and Feeding Habits</u>.- *D. grisea* larvae were always found associated with decaying algae that had turned yellow-green or with algae covered with debris. Unlike chironomid larvae their ability to construct dwelling tubes out of debris and algal filaments is limited, and for this reason they live in rudimentary tubes somewhat exposed, among algal filaments.

During feeding, the larvae put their heads outside the tubes and scrape off debris and dead leaf or algal tissues with their mandibles, working the food backwards to the gut with to-and-fro movements of the pharynges. On detecting the slightest movement, they retract backwards into their tubes and remain there until no further movement is detected, after which they once again resume feeding.

b). Locomotion. - Larvae of D. grisea are not capable of swimming in open water but can move fairly rapidly through algae, much in the same way as P. slossonae and B. glabra. When pursued to the edge of the algal mat they drop off the edge to the bottom and in this way escape their predators.

c). First Instar. - First-instar larvae were collected in low numbers from May 25 to June 5 and again on July 7, 14 and August 17. The greatest numbers occurred on May 27 (Table 11, Fig. 62). First instars are relatively small and difficult to find, especially in thick algae containing a quantity of debris and mud. Their overall lengths, for 13 individuals measured from hatching to the end of the stage, vary from 0.60 to 1.13 mm. and their widths 0.05 - 0.08 mm. Their head capsule lengths and widths vary from 0.47 - 0.50 mm. and 0.26 - 0.27 mm.

Unlike P. slossonae and B. glabra larvae, D. grisea larvae do not appear to be associated with any particular type of algae but more frequently occur in algae with some amount of decay, generally in algae covered with some debris. D. grisea larvae will feed soon after hatching.

The duration of this stage under laboratory conditions (70°F. and 50 per cent R.H.) based on the rearings of 91 first instars, was 4 - 13 days, with a mean of 7.5 days.

d). Second Instar. - Second instars were collected from May 27 to

September 12, 1964, the greatest numbers occurring on June 2 (Table 11, Fig. 62). The overall lengths for 23 individuals ranged from 1.04 - 1.92 mm. and their widths 0.08 - 0.14 mm. Their head capsule lengths and widths varied from 0.71 - 0.75 mm. and 0.36 - 0.40 mm., respectively.

The duration of this stage under laboratory conditions ranged from 4.5 to 15.5 days with a mean of 6.5 days for 126 individuals studied.

e). Third Instar. - Third instars were collected throughout the sampling period, with greatest occurrence taking place on June 5 (Table 11, Fig. 62), three days following occurrence of the second instar. The overall lengths for 23 individuals examined during the stadium varied from 1.71 - 3.08 mm., and widths 0.12 - 0.23 mm. Head capsule lengths and widths ranged from 1.04 - 1.13 mm. and 0.53 - 0.59 mm., respectively.

The duration of this stage under laboratory conditions was 4.5 to 18 days, with a mean of 6.5 days for 203 individuals experimented.

d). Fourth Instar. - Fourth instars were collected throughout the sampling period, May 25 - September 12, but occurred in greatest numbers on June 9 (Table 11, Fig. 62), four days following peak occurrence of the third instar, and also on July 20. Overall lengths for 10 individuals range from 2.70 - 4.50 mm. and their widths from 0.20 - 0.30 mm. Their head capsule length and width vary from 1.43 to 1.59 mm. and 0.75 to 0.86 mm., respectively.

Under laboratory conditions the fourth-instar stage lasted 5.5 to 22 days, with a mean of 7.3 days for 194 individuals studied.

3. Pupae.

Pupae were obtained in samples taken on May 27, 30, June 9, 24, 30

July 20 and August 17 (Table 11), suggesting that there were several generations of D. grisea between May and September, 1964.

D. grisea pupae are pale to light brown just after pupation but turn chocolate to dark brown in colour after one day. Following pupation, pupae remain for some time within the larval tubes but eventually work their way to the surface of the water where they soon emerge as adults. The pupal period under laboratory conditions averages 2.5 days in contrast to Thomsen's (1937) observation of 5 days.

The lengths and widths of D. grisea pupae, unlike those of P. slossonae and B. glabra vary imperceptibly between the two sexes, there being no sexual dimorphism. These range from 2.12 - 2.93 mm. and 0.42 - 0.54 mm. in the male and respectively 2.13 - 3.08 mm. and 0.44 - 0.53 mm. in the female.

4. Adults.

Unlike the predator species P. slossonae and B. glabra, sexual dimorphism in D. grisea is indistinct, the males being only very slightly larger than the females. Their overall lengths, excluding antennae, range from 1.94 mm. to 2.19 mm. in the male and 1.58 - 1.92 in the female.

Again, unlike the predator species, D. grisea adults can be maintained in the laboratory for a longer period (5 - 7 days) on 10 per cent sucrose and their eggs will mature on this diet alone.

Such eggs, however, do not hatch since they are not fertilized.

Like P. slossonae and B. glabra this species does not mate in confinement and in nature it probably mates in a swarm.

VIII. DISCUSSION

A. BEZZIA GLABRA (COQUILLETT)

The seasonal distribution of *B. glabra* appears to be bimodal for every stage in both sites A and B (Figs. 52 - 57). The occurrence of the pupae and adults in May - June and July - August, suggests that for this species there are two generations per year. Larvae were obtained throughout most of the sampling period, in two more or less distinct periods, and one peak per stage. Thus, first-instar larvae occurred mainly during the periods, June - July and August - September with only one peak on June 6 (Fig. 52); second-instar larvae in July and in August - September with one peak on July 20 for site B and July 27 for site A (Fig. 53); third-instar larvae in May - June and July - September (Fig. 54), with a single peak in early August; and fourth-instar larvae (Fig. 55) one peak on May 18 in site A and on August 25 in site B, during the period May 13 - September 12. However, when the data on *B. glabra* for sites A and B were combined (Fig. 58) only one generation per year was indicated.

The bimodal distribution of *B. glabra* resembles that of *Culicoides impunctatus* Goetghebuer (Kettle, 1950). In *C. impunctatus* Kettle (loc. cit.) concluded that two races were involved at Loch Lomond in England, and that the bimodal seasonal distribution could not be due to climatic factors or the bivoltine nature of *C. impunctatus*. In *B. glabra* laboratory rearing of their larvae reveals that the duration of each stage varies considerably according to the availability and amount of food consumed. Larvae that were fed regularly and to satiation completed their life cycle considerably faster than those which were alternately starved and fed. This difference in duration of the larval stages with difference in food supply explains the occurrence of these stages over most of the sampling period. The seasonal distribution of B. glabra therefore appears to be as follows. Eggs laid in June hatch out in approximately one week into first-instar larvae with peak in early July (July 6), followed two weeks later by second-instar larvae (peak around July 21), two weeks later again by third-instar larvae (peak on August 3) and finally followed three weeks later by fourth-instar larvae, (peak on August 25). Most of the fourth-instar larvae together with a fair number of third, and fewer second and first, pass through an obligatory diapause in winter. In the laboratory, larvae do not feed during the winter even at a temperature of 70°F. In spring, third-instar larvae moult to the fourth instar, and the latter reach their peak on approximately May 20. Field data indicates that fourth-instar larvae pupate in late May and early June, and that adults emerge about four days later. Soon after emergence the adults feed and mate and fertilized eggs are deposited in about a week. Eggs are laid during a period of several weeks.

The annual life history is summarized by a survivorship curve (Fig. 59).

B. PALPOMYIA SLOSSONAE (COQUILLETT)

The seasonal distribution of P. slossonae in all its stages resemble that of B. glabra rather closely, for both sites A and B (Figs. 43 - 49). As in B. glabra, there is only one generation per year although occurrences appeared in two distinct periods for most stages (Fig. 50).

As in *B. glabra*, *P. slossonae* overwinters mostly in the third and fourth larval instars. Overwintering third-instar larvae moult to the fourth instar in May, pupate, and give rise to adults in late May and early June. Eggs are laid in June and the cycle repeated (Fig. 51).

In both *B. glabra* and *P. slossonae* the two peaks for each larval stage, a large followed by a small, are likely due to random sampling variation (Cole, 1956) and cannot be taken as indicative of the presence of two generations or even two biological races (contra Kettle, 1950). In the adults, however, the peak period are separated by about 1½ months and indicate two possible generations. Yet, laboratory rearings show that the life cycle of both species cannot be completed within such a short time. It would appear, therefore, that the occurrence of *P. slossonae* and *B. glabra* adults in May - June and July - August is due to the phenomenon of synchronization involved in seasonal emergence of aquatic insects (Corbet, 1964), discussed below.

The occurrence of *P. slossonae* and *B. glabra* adults in May - June and July - August parallels the appearance of two peaks of biting midges in 1962 - 1963 in Turkmenia in Russia (Muradov, 1965). This author found that in the Kopet-Dagh regions biting midges, particularly *Culicoides puncticollis* Becker and *C. schultzei* Enderlein, were troublesome biters from the middle of March to the middle of November but were particularly so in May - June and, most significantly so in August - September.

SEASONAL EMERGENCE

Seasonal emergence of *P. slossonae* and *B. glabra* is typical of insects in temperate regions (Corbet, 1964) with rainfall and temperature imposing the greatest seasonal variation. The temporal pattern of emergence in both *P. slossonae* and *B. glabra* is similar to that of the dragonfly *Anax imperator* Leach (Corbet, 1957) in which (i) the majority of a year-group overwinter in the final larval instar and respond synchronously to rising temperatured in the spring, and (ii) a small percentage enter the final instar after May, postponing metamorphosis until the following year. In the dragonfly *Aeshna cyanea* (Müller), Corbet (1959) and Schaller (1960) (vide Corbet, 1964) found no such rigorous control of the density of the overwintering larvae. These larvae can overwinter in several instars and still emerge the following year.

On the basis of specific responses being involved in such seasonal regulation, an ecological classification of British Odonata has been attempted from inspection of the shape of emergence curves and from the degree of correlation between synchronization of emergence and the number of larval instars which can precede emergence in one year. Two major types were recognized: 'spring' and 'summer' species (Corbet, 1954, 1964). According to this classification, spring species were defined as those which possessed a diapause in the final instar larvae and summer species as those which did not. Corbet (1964) redefined spring species as "those in which all, or a majority, of a population spends the winter before emergence in the final larval instar". Summer species, a heterogeneous group, were divided further into two groups according to the normal duration of larval development (Carbet, loc. cit.): (a) univoltine species, and (b) species requiring more than one year to complete a generation.

Following the above classification, *P. slossonae* and *B. glabra* can be defined as spring species and this designation, the first to date for any ceratopogonid, promises to be an ecological aid in the systematics of the midges. Similar classifications of aquatic Ceratopogonidae should be undertaken, especially for the higher forms with worm-like larvae, as for the British dragonflies.

C. DASYHELEA GRISEA (COQUILLETT)

Under laboratory conditions D. grisea completes its life cycle from egg to adult in about one month, approximately the same period of time as that taken in the field, e.g. May to early July (Fig. 62).

Eggs were collected from May 25 to June 2 in site A and from May 25 to 30 in site B and were evidently present in both sites prior to May 25. First-instar larvae were collected from May 25 to June 5 and on July 7, 14 and August 17 (Table 11), with greatest numbers occurring on May 27. Second-instar larvae were collected throughout the period of sampling (Table 11) but only one peak occurred on June 2. Third and fourth instars were also collected throughout the period of sampling, with the greatest numbers obtained in site A on June 15 and July 20 respectively and in site B on June 5 and 9 respectively.

An examination of the data obtained in sites A and B (Figs. 60, 61; Tables 9, 10) shows that D. grisea has three generations per year and overwinters mostly as second-, third- and fourth-instar larvae. The first generation lasts from late May to early July; the second from early July to about the end of July (site B) or early August (site A); the third from the end of July or early August to the following May.

In both sites, the duration of the first generation is well marked but that of the second and third is not. The irregular oscillations obtained for the second and third may be due to the sampling of these generations weekly instead of every three days as in the first generation. D. grisea stages are of short duration and weekly samples may not provide data on peak emergence of its stages. Another possibility is that the low numbers of D. grisea obtained during the second and third generations reflects active predation by the predators P. slossonae, B. glabra, and also a pelopiinid chironomid of the genus Pentaneura which also prey on both P. slossonae and B. glabra. This is a real possibility since predation by B. glabra and P. slossonae was low during May - June when the preferred chironomid larvae were abundant (Fig. 63), and high from July to late August when chironomid larvae were few.

In site A the first generation lasted somewhat longer than that in site B and may have been due to variation in amounts of food available between the two sites as well as amounts of energy expanded in obtaining food. As mentioned in an earlier section, site B is considerably richer than site A in organic debris, the chief and perhaps only food source of D. grisea larvae. This accounts for the significantly higher number of eggs laid in B and the higher larval populations here. Site B is also more muddy than site A and harbours less of the predator species than A, presumably because the latter species with their large, well-developed, pigmented eyes, prey to some extent by sight.

RHYTHMIC EMERGENCE

Emergence is rhythmic if it occurs periodically in cyclical fluctuations, the latter characterizing the rhythm. According to Remmert (1962) the most widespread emergence rhythms have a diel periodicity. This is typically regulated and maintained by an 'internal clock' (the endogenous or circadian rhythm) which is 'set' by responses to external time-cues (exogenous factors) (Corbet, 1964). Such a rhythm is considerably stable and independent from atypical fluctuations in the environment due to interaction of endogenous and exogenous components.

Most insects studied show emergence rhythms with a lunar periodicity and with the exception of the dermestid beetle, Anthrenus verbasci (L.) (Blake, 1959), no insects exhibit a rhythm with a period exceeding a lunar month. Among the Ceratopogonidae, marine forms living in the tidal zone where direct or indirect lunar effects might be expected, have been known to exhibit rhythmic emergence -- Culicoides pelilioùensis Tokunaga (Tokunaga & Esaki, 1936) which inhabits mangrove swamps of the Palau Islands and several Australian Culicoides species. In Australia, Reye and Lee (1963) found Culicoides subimmaculatus Lee and Reye and C. ornatus Taylor with fortnightly emergence peaks taking place about the time of the half moon, i.e. at the neap tide, apparently depending on the period of exposure of an emergence zone just above neap tide level. They also found that C. marmoratus (Skuse) which occurs at a higher level, has a longer and less dramatic rise in numbers, and C. molestus (Skuse) and C. immaculatus Lee & Reye seem to be dependent on different phases of the tide cycle, possibly related to duration of exposure of lower levels, or to tidal stranding at higher levels of pupae which become free floating at this time. The last case is similar to that of the marine chironomid, Clunio marinus Haliday, which inhabits the shores of the North Sea. In this species, Caspers (1951) found that emergence is restricted to two periods in each synodic month, occurring within a few days of new and full moon respectively, and that emergence coincides with the times of low tide when algal mats (in which the early stages dwell) are exposed, and when, accordingly, emergence is less hazardous.

It is interesting that lunar rhythms of emergence also occur in several insects inhabiting inland freshwaters where no indirect effects of the moon can be discerned. Corbet (1958) studied several insects in Lake Victoria and found these species to differ with respect to the position of peak (or peaks) emergence in the synodic month, and synchronization of peaks. Several authors have suggested that such lunar emergence rhythms of aquatic insects could result simply from the fact that the duration of a generation is an exact multiple of a lunar month, but Corbet (1964) has shown that emergence rhythms can be explained only on the assumption that some synchronizing factor operates during development.

The proximate and ultimate factors controlling lunar emergence rhythms in freshwater insects are not obvious. The work of Rowe (1958) (vide Corbet, 1964) on the mayfly _Povilla adusta_ Navas, suggests that response to photoperiod in early larval life is a possible proximate factor, and Corbet (1964) concludes that "most lunar insects in non-tidal waters use variants of the same system" as those in tidal waters, e.g. lunar cycle of rainfall discovered by Adderley and Bowen (1962). Corbet (loc.cit.) points out that ultimate factors might be of two kinds: (i) those concerned with the direct effect of physical factors on the emerging insects, e.g. periodicity of rainfall and nocturnal illumination, or (ii) those related to the phenomen of synchronization _per se_, e.g. concerning the regulation of predation and density.

On the basis of the data obtained in the present study, it is concluded that D. grisea exhibits rhythmic emergence -- the first ceratopogonid species of inland freshwaters reported to do so.

D. PREDATOR - PREY INTERACTION

Since chironomid larvae and pupae constituted the main food items of both P. slossonae and B. glabra, and since all species of chironomids were preyed upon, the total number of the prey obtained at each sampling throughout the period, May 25 to September 12 (Table 12) was plotted on a graph (Fig. 63) along with total larval counts for P. slossonae and B. glabra combined. The total counts of the less preferred prey, D. grisea, are not included with those of the chironomid species since they were too low to significantly cause any change in the population fluctuations of the combined prey species. Besides, D. grisea does not appear to be the normal food of the predators.

On the graph, chironomids showed two peaks, one May - June and one August - September, and predators two peaks also, the first in June which coincides with the chironomid peak, and the second in June - August which does not (Fig. 63).

There seems to be no adequate explanation for this incongruous behaviour of the predator populations with respect to prey populations save for the counts missed in site B on June 24 and 30 and in site A on July 21. Assuming that the counts missed would not significantly alter the pattern of distribution, from the graphs it would appear that each individual predator had in early June only about 1½ specimens to feed on, i.e. assuming the predatory ability was the same for all individuals. This low number of prey per predator would at first sight appear insufficient to sustain the predator species but as mentioned in a previous section, predators during this period

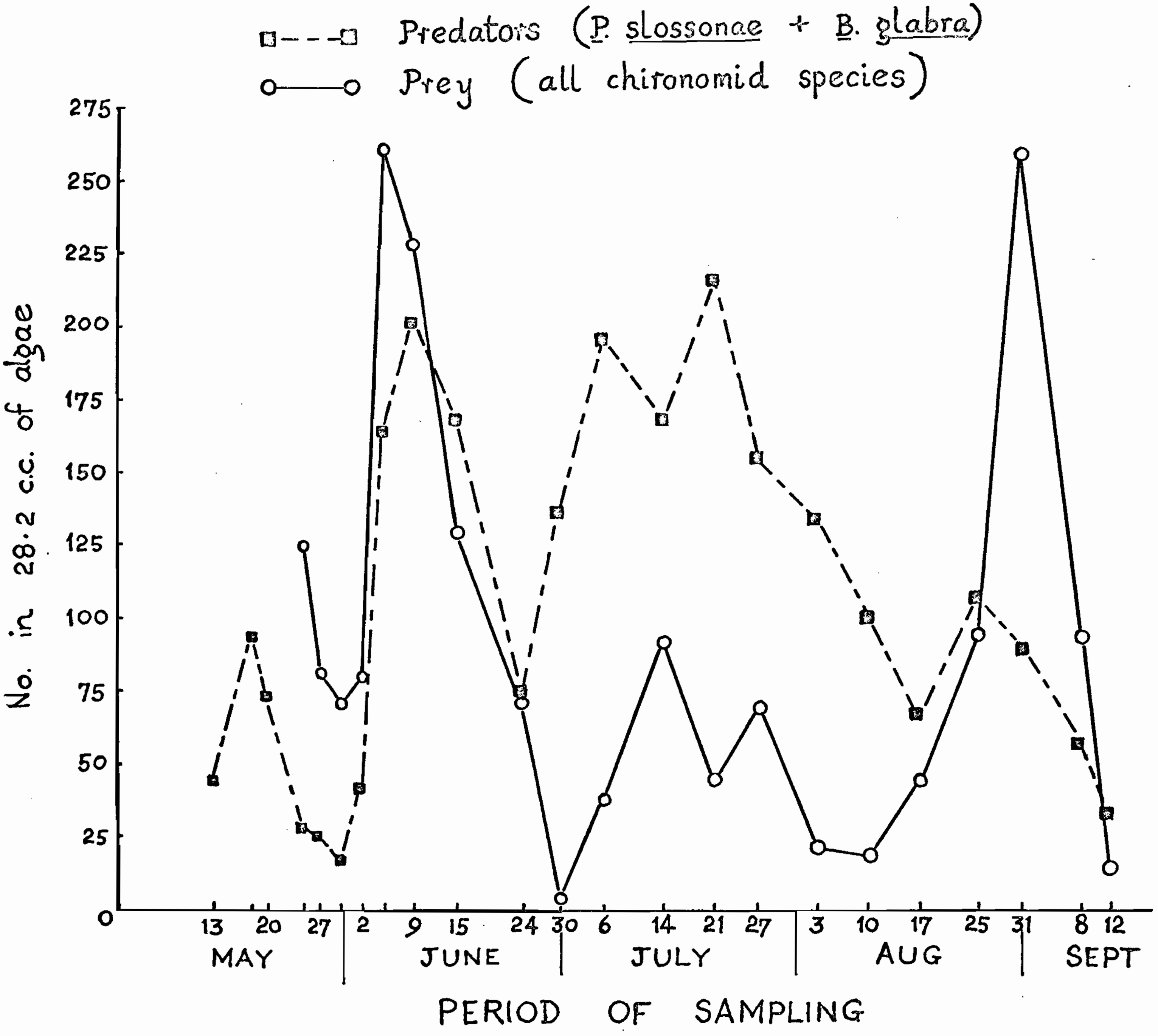


Fig. 63. Seasonal fluctuations of predator and prey densities

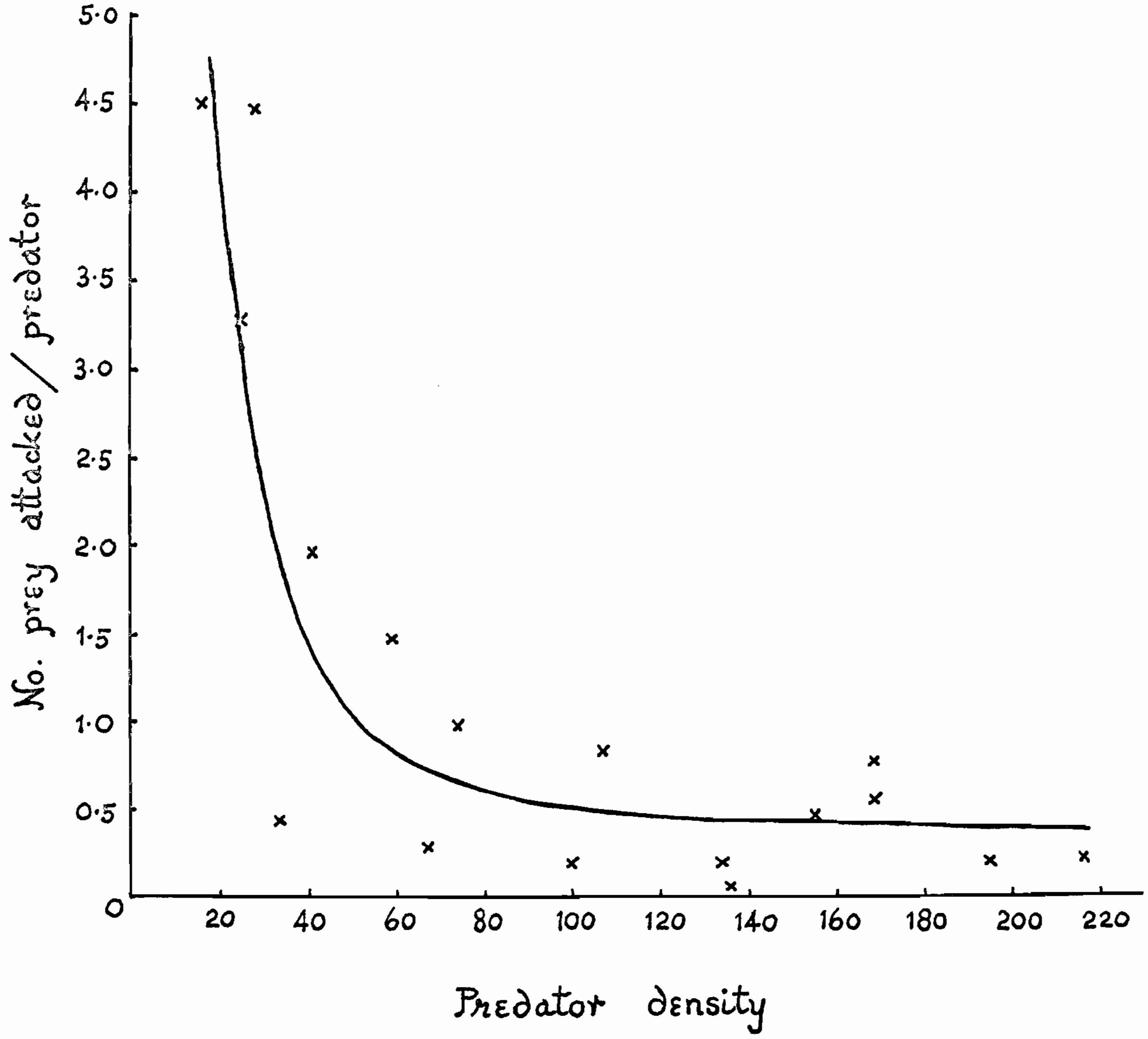
were mainly first-instar larvae which stage requires only low numbers of prey for survival. During the period July - August, each predator had less than half a prey to feed on at any one moment. Such a starvation diet would in all likelihood result in intense intra- and inter-specific competition for prey, and cannibalism would also be resorted to. Also during this period, the less preferred types of prey like D. grisea larvae and pupae and crustacea, would be attacked. These contentions appear to be borne out as shown by the sudden fall in numbers of D. grisea during this period (Figs. 60 - 62) and the drop to a low level of the predator populations in the middle of August, especially on August 17. Coincident with this fall in predator numbers was the rapid rise in prey population in August - September, followed by another rise in predator numbers which again resulted in a sudden decrease in prey populations.

The population behaviour of the prey and predator species during the May - June period is a direct numerical response similar to that reported by Holling (1961) for small mammalian predators (cinereous shrew and deer mouse) on insects (Neodiprion setifer (Geoffroy)). The predator population increases and decreases with an increase and a decrease respectively in the prey density. The June - August period, however, does not follow any known type of numerical response. It would appear to be an inverse numerical response like that reported by Morris et al. (1958) for the spruce budworm and certain birds (magnotia, myrtle and black-throated green warblers) but in Morris et al's example, the predator density was low when the prey density was high. The factors which caused the maintenance of high predator density a great decrease in prey density, are not known. The most probable explanation is that the predators have the ability to withstand hunger and starvation over long periods and can switch on to other types of prey when in need.

When the number of prey attacked per predator (Table 13) is plotted against the predator density, a hyperbolic curve is obtained (Fig. 64). This is similar to the laboratory findings of DeBach and Smith (1947) for the housefly Musca domestica Linnaeus attacked by the parasite Nasonia vitripennis (Walker). They found that the number of housefly puparia attacked per parasite decreased as the density of parasites increased, the rate of increase being most rapid at low prey densities. The same functional response to predator density has been obtained in laboratory experiments for three other species of parasites, a chalcid, a braconid and an icheumonid (Holling, 1961), and in nature by Miller (1959, 1960) for the parasites Apanteles fumiferanae Viereck and Glypta fumiferanae (Viereck) in the spruce forests of New Brunswick.

As explained by Holling (1961), "the two components, exploitation and interference adequately explain those response curves the slopes of which decrease continuously as predator density rises". The exploitation component arises from competition by predators for the same resource. Consequently, as the density of predators increases the chance that any individual predator will discover a prey that has not already been discovered decreases. The interference component also arises from competition for the same resource and from cohabitation in the same environment and becomes progressively more important as predator density rises and contacts among predators become more frequent. A better knowledge and understanding of both the functional and numerical response of the predator population to changes in prey density will be obtained if more is known about the

Fig. 64. Functional response to predator density



competition for food between predators. As it is, very little is known about this (Klomp, 1964, Holling, 1961).

E. INTERSPECIFIC COMPETITION BETWEEN PALPOMYIA SLOSSONAE AND BEZZIA GLABRA

P. slossonae and *B. glabra* can be considered as ecological homologues according to the definition of De Bach and Sundby (1963) since both species, as far as can be determined, have identical ecological niches, and co-exist together in a habitat of specially identical ranges. From the distinctly different numbers obtained for early stages of the two species in 1964, it may be assumed that competitive displacement between these homologues, i.e. elimination of *B. glabra* by *P. slossonae* has been taking place.

Competitive displacement between ecological homologues, known also as Gause's Law and the Competitive Exclusion Principle, is defined and reviewed in detail by De Bach and Sundby (1963). The main points are:

(1) Volterra (1926), Lotka (1932) and Haldane (1924) concluded from mathematical treatment of interspecific competition that when two ecological homologues compete, one will be displaced or eliminated. This conclusion was confirmed by Gause (1934) whose experiments on competition between *Paramecium aurelia* Müller and *Paramecium caudatum* Ehrenberg, led to the enunciation of Gause's Law. Crombie's (1945, 1946) experiments with graminivorous insects also confirm the conclusion.

(2) Gause's Law or Hypothesis holds only under certain conditions. It does not hold when characters of the habitat are altered. Park (1945, 1948), for example, found that in the interspecific competition

between Tribolium confusum Duval and T. castaneum (Herbst) the winner is not always the same species, competitive displacement being dependent on characteristics of the habitat, like temperature and enemies. Utida's (1953) experiments with two species of bean weevils, Callosobruchus quadrimaculatus Fabricius and C. chilensis Linnaeus, show that two species having the same food requirements can coexist indefinitely in the same habitat when their numbers are controlled by parasites or predators but one will eliminate the other without parasitism as in his experiments where C. quadrimaculatus in the absence of parasites completely eliminated chinensis by the fifth generation but coexisted indefinitely with the latter species when controlled by the parasitic pteromalid wasp Neocatolaccus mamezophagus which prefers equally the larvae of both host species.

(3) The assumption is implicit in Gause's Law that two species however closely related and however similar in habits, have inherent biophysical differences which will favour one over the other in a particular situation. It is also assumed that immigration of the weaker species does not occur.

(4) Absolute food shortage is not necessary for competitive displacement to occur for three Aphytis species for example (De Bach and Sundby, 1963)

(5) In any paired interspecific competition, the species with the highest number of F_1 progeny is the winner under unchanging conditions (De Bach and Sundby, 1963).

Interspecific competition between P. slossonae and B. glabra appears to confirm the above points. It is however not determinable from short term studies whether P. slossonae will ultimately eliminate B. glabra since the duration of their coexistence has not been determined. It might appear from the findings of Utida (1953) that P. slossonae and B. glabra might coexist indefinitely since both species are to some extent controlled by predators and possibly parasites. From observations of the samples collected, larvae of one large species of pelopiinid chironomid of the genus Pentaneura, with large mandibles and large, bifid, prothoracic and anal pseudopods was occasionally seen to feed on larvae of both P. slossonae and B. glabra and other chironomid larvae. The number of this only carnivorous species of chironomid in the habitat was usually very low. Both P. slossonae and B. glabra were observed to feed on this carnivorous chironomid so that there is a degree of mutual control in populations of these three predators.

Parasites have not been observed in the ceratopogonid species studied, but Becker (1958) has recorded bacteria, ciliates and mites as parasites of Culicoides species. Epizooites were observed to occur in large numbers on B. glabra larvae. Their exact identification has not been determined but from examination under the high-power microscope they appear to be ciliates close to the genus Zoothamium. The protozoan is tree-like and branching is dichotomous throughout, each branch terminating in a microzooid. The protozoa are usually found attached to the ends of the host, i.e. on the head, first and last segments of glabra larva. They do not appear to cause any harm, living apparently as commensals and benefiting through transportation by the host. Whether phoresy here is permanent or transitory is not known but more likely permanent since they do not detach themselves when treated with chemicals or heat. They may however prove to be possible ectoparasites which could harm the insect host. Regulation of the host density by the protozoan could conceivably be a factor contributing to the degree of coexistence between *B. glabra* and *P. slossonae*.

IX. CONCLUSIONS

It may be concluded, from the sampling data, that *D. grisea*, *B. glabra* and *P. slossonae* show a similarity in population behaviour in two essentially dissimilar pond habitats. This suggests that the inter-relations between the component organisms of the pond community studied, are relatively uniform throughout and likely constitute a dynamically stable system. Confirmation of this can only be obtained through long-term studies. From the number of eggs laid per batch per species, it is clear that the power of multiplication is great for these species but from the optimum population densities obtained for the species it is also clear that the mechanisms of control in these populations are effective. One of the most important regulating mechanisms noted is the food-cycle structure of the community. For these three species in the community food-supply and more significantly, predation, acted as limiting factors, with reproductive limitation, fixed by heredity, also of great importance. Other important factors, such as inter - and intra-specific competition, which were more variable, also acted as major controlling mechanisms (Klomp, 1964).

It was found that *P. slossonae* and *B. glabra* are ecological homologues competing for the same natural resources , but as the former species has a higher fecundity and higher F_1 progeny, it is accordingly the stronger competitor (De Bach & Sundby, 1963), and from the data collected, appears to be in the process of eliminating *B. glabra*. However, a chironomid predator which acts on both these species and a suspected protozoan ectoparasite of *B. glabra*, may prove to be the regulating factors that allow these two species to coexist indefinitely (cf. Utida, 1953). Also chironomid larvae constitute the main food source of the two ceratopogonid predators except during the period late June to August when alternative food sources must be available to prevent the elimination of the predators. The only proven prey, D. grisea, however, does not appear to occur in sufficiently high numbers to maintain the predator species through this period. The high numbers of the predators during June - August must then be explained by some other factors; e.g. possibly the ability of the predators to withstand hunger which, laboratory experiments show, is considerable, or survival of the predators through cannibalism which, however, appears to be limited.

The emergence pattern of the two ceratopogonid predators is seasonal and that of the prey, D. grisea, rhythmic, but emergence in both types involves the phenomenon of synchronization. Synchronization of emergence has not been looked upon as an important factor in the regulation of population numbers. The writer wishes to suggest that it might be of very great importance and implication. Corbet (1964) has considered and cited some of the more evident consequences of restricted emergence and has pointed out indirectly the effect of (i) seasonal position of the emergence period and (ii) the synchronization of emergence within the emergence period, on population numbers.

The seasonal position of the emergence period will determine the physical and biotic environment that adults encounter since temperature and duration of day, night and twilight on the one hand will affect the type and pattern of adult activities, and the coincident plants will be available for emergence supports, shelter or sites for swarming, oviposition and the demarcation of territories, on the other hand (Corbet, loc. cit.). In the latter also, the coincident animals will determine the amount of predation or parasitism which occurs, the density of interspecific competition for available shared resources, and for species poor in sexual recognition, the influence they have on frequency of abortive sexual interaction or interspecific crossing.

Synchronization of emergence within the emergence period has consequences which increase both survival and mortality, and might prove to be of selective and adaptive value in several ways (Corbet, 1964). Rhythmic emergence, for example, might tend to become established in a population from time to time simply because individuals carrying a gene which tied emergence to a certain moon phase would mate with each other more often than with others not so endowed. In other words, the adaptive value of synchronization resides in the greater opportunities for mating which it provides. Synchronization is therefore expected to be developed best in insects whose adults are short-lived and spatially dispersed. Coincidence of the sexes, especially in these rare and short-lived species is necessary if reproductive potential is to be realized. In the Ceratopogonidae Downes (1955) has suggested that swarming is a means of bringing dispersed males and females into close proximity and, if the markers are specific, functions as an isolating mechanism. But, intraspecific encounters, leading to dispersal or interference with mating and oviposition, can provide a homeostatic device which limits population size (Corbet, loc.cit.) Wynne-Edwards (1962) has suggested that aggregation before reproduction is a device which presents an arena for intra-specific competition, resulting in the consequent dispersal of the less successful individuals. An example of this has been found in the dragonfly Libellula quadrimaculata by Frankel (1932).

Synchronization of emergence, depending on the environment, may increase or reduce predation. For example, Martin (1895) and Lyon (1915) found that mass emergence of gomphid dragonflies along a river bank may attract large numbers of non-territorial birds to feed on them, and Corbet (1957) found that where a pair of birds successfully defends a territory which includes an emergence site, mass emergence reduces mortality when more individuals emerge than can be eaten in a single day.

Population ecologists belong primarily to two opposing schools: one holds the view that there is a real regulation of numbers by feed-back mechanisms and the other that such mechanisms are not in operation but that numbers fluctuate between relatively narrow limits because of the ever-changing influence of one or more (or a complex of) environmental factors. Essentially this means that population regulation is due to either some factors intrinsic and inherent in animals populations or to external environmental factors. It would appear that both schools of thought are necessarily correct since the one is intimately related with the other. From teleological and evolutionary considerations, this would be so since the environment first existed before organisms arose to occupy it. Therefore logically speaking, organisms after having arisen must adapt themselves to the limitations of the environment in order to maintain and perpetuate themselves. Environmental factors therefore control the behaviour of animal populations. But through adaptation and natural selection animal populations gradually become less affected by environmental factors as they acquire genitic and physiological mechanisms to overcome their ever-changing influence, so that their behaviour becomes less affected by changes in the environment. The influence of the environment on the behaviour of animals becomes increasingly smaller as animals become more and more highly evolved. In man, control of his behaviour by environmental factors is overcome by his ingenuity.

In insects, however, population behaviour is largely influenced by environmental factors as we have seen in the considerations of the patterns of emergence in aquatic insects. Synchronization of emergence is a consequence of the necessity for short-lived, rare species to encounter one another so that coincidence of the sexes brings about fruitful mating and thus increases reproductive potential. But on the other hand, it acts as a homeostatic device in limiting population size by encouraging dispersal or interference with mating and oviposition. Furthermore it is of adaptive value in the regulation of predation and density by having consequences which increase both survival and mortality. In non-aquatic insects and other animals other types of mechanisms influenced by environmental factors might be operating to regulate population numbers (Klomp, 1964).

In the present study it is interesting to note that in the predator species, B. glabra and P. slossonae, a large percentage of adults emerging synchronously in spring (early June) had spent their last winter in the final larval instar which they had entered the previous autumn. A small percentage however had spent the winter in the penultimate instar and these entered the final instar before June so that they spent only about 45 days instead of nine months in the final instar. This second group emerged later (July - August) and showed poor synchronization. The pattern of behaviour in both species seems to suggest that the occurrence of two emergence periods instead of one per year is related to a shift from more to less prolific genotypes in the population and vice versa, induced by an increase in density. Such behaviour would then constitute regulation through a genetic feed-back mechanism (for detailed information see Pimentel, 1961; Wellington, 1957, 1960).

In the final analysis, animal populations appear to be regulated by a set of very complex factors operating independently or in groups, and only a quantitative study involving all branches of biological science of species living in a community or, better in an ecosystem, can provide an understanding of the factors and mechanisms that bring about regulation. Detailed studies on single species only provide information on the particular species. Information on the interrelations among individuals of the same community and of the ecosystem can only be obtained from studies of all species involved. But this would require the joint cooperation and effort of many scientists.

SUMMARY

I. SYSTEMATICS

1) A thorough treatment of the systematics of the subfamily Forcipomyiinae based on all available knowledge of the group is presented for the first time, and the classification of the group revised; a detailed diagnosis of the subfamily Forcipomyiinae is given and keys to the genera, subgenera for all stages are created for the first time.

2) Eighteen species of Forcipomyiinae of which 16 are described as new are treated from a morphological and systematic point of view.

3) The typological-morphological species concept, used as a practical taxonomic basis in previous descriptions, is discussed and considered to be inconsistent with the theory of evolution and obsolete in the light of modern taxonomic applications.

4) The weaknesses of previous taxonomic approaches to the Ceratopogonidae are pointed out. Improvements of these are implemented by (i) describing every species in all stages, (ii) erecting new terminologies for detailed quantitative measurements of all taxonomic characters of immature stages, giving the mean, standard deviation and standard error for a reasonably large number of specimens measured in all stages, and (iii) giving well-illustrated figures of all important taxonomic characters of all stages. Non-morphological characters are considered to be of equal taxonomic value as morphological ones and are proposed for inclusion in all future taxonomic descriptions.

The quantitative approach is adopted as it has the following advantages over the hitherto largely qualitative approach: (i) it is scientifically accurate and precise and removes ambiguity almost invariably encountered in a qualitative treatment, (ii) it enables the collection of data that would ultimately lend itself to the separation of sibling species by the discriminant function, (iii) it provides a means whereby systematic relationships between species can be determined.

5) Confusion in the use of terminologies with particular reference to male genitalia, and of exact measurement of taxonomic characters, is clarified.

6) The systematic position of *Thyridomyia* and *Atrichopogon* in relation to a new species of *Thyridomyia*, is discussed from considerations of morphological characters in the Forcipomyiinae.

7) The geographical distribution of the Forcipomyiinae is compiled and presented for the first time and the Oriental Region is found to be the most likely centre of evolution and radiation of the group.

8) The phylogeny of the Forcipomyiinae is presented for the first time and considered primarily (not exclusively) from male genitalic structures and comparative morphology of all stages. Primitive and advanced characters of the family Ceratopogonidae are discussed, and phylogenetic relationships between all genera and subgenera of the Forcipomyiinae, given. A dendogram showing the phylogeny of the Forcipomyiinae and figures showing the evolutionary trends in claspette development within the family Ceratopogonidae are given.

The genus *Atrichopogon* is shown to be the living prototype of all Ceratopogonidae despite its many advanced features.

II. ECOLOGY

1) A quantitative ecological study of the life history of three aquatic species of ceratopogonids, *Palpomyia slossonae* (Coquillett), *Bezzia glabra* (Coq.) and *Dasyhelea grisea* (Coq.) is given for the first time. Studies were carried out in a pond at Morgan Arboretum, Macdonald College, Quebec.

2) The experimental plot, sampling procedure, sample unit size and the timing of sampling are discussed and given.

3) Sampling was carried out from May to September, 1964, in two sites, A and B: thrice weekly during May - June; once weekly thereafter. At each sampling, twenty 1.41 cc. of algae samples were collected and examined under the binocular microscope for all stages of midge and chironomid species. It took two persons 20 minutes each to examine and count specimens per 1.41 cc. sample.

4) Egg masses and early larval instars were reared in the laboratory and their life cycle and habits noted. Chironomid larvae, collected twice to three times a week and reared in the laboratory on blanket algae, served as food for the ceratopogonid predators.

5) The seasonal distribution of *P. slossonae*, *B. glabra* and *D. grisea* was found to be basically similar in both sites A and B, thus showing structural composition of the pond to be generally homogeneous.

The two predator species, *P. slossonae* and *B. glabra*,have one generation per year, overwintering mainly in the last larval stage and emerging as adults in May - June and July - August. *D. grisea* on the other hand, has three generations per year, overwintering mainly in the second-, third- and fourth-instar larval stage. P. slossonae has a higher fecundity than B. glabra, the former laying about 300 eggs per batch on the average and the latter about 200. Eggs are laid a few days after adult emergence in May and hatch a few days following oviposition. The duration of each larval instar is about a month for both species. Pupae of P. slossonae last 3.9 days and those of B. glabra 2.3 days.

D. grisea eggs per batch average 72. They hatch a few days following oviposition. Each larval stage lasts about a week and the pupa lasts 2½ days. Each generation thus lasts approximately one month.

6) Two temporal patterns of adult emergence were observed: seasonal (P. slossonae and B. glabra) and rhythmic (D. grisea). The significance of these emergence patterns in population regulation, especially with regard to synchronization, is discussed. The type of emergence curves was found to be important in the classification of aquatic Ceratopogonidae.

7) Predator-prey interaction and interspecific competition between P. slossonae and B. glabra are discussed. The two predator midges feed on all chironomid species in the pond (including a predator chironomid of the genus Pentaneura which feed on both midge predator species) and also on D. grisea, but they prefer chironomids to D. grisea. During starvation both species exhibit cannibalism and mutual interspecific predation.

The total amount of food available to the midge predators appeared inadequate throughout the sampling period. The survival of both species must be attributed to their ability to withstand hunger, to cannibalism, or their using food substitutes. As the fecundity of P. slossonae is higher than that of B. glabra, interspecific competition should, according to De Bach & Sundby (1963), result in the eventual extermination of the latter species. The presence of a pelopiinid predator, Pentaneura sp., feeding on P. slossonae and B. glabra (and also D. grisea and other chironomids) could conceivably account for the successful coexistence of the predators in the pond (cf. Utida, 1953).

III. TIME SPENT ON PROJECT AND ORIGINALITY OF THESIS

The present study involved a considerable amount of time and concentration. In the course of this study, the author has spent about 7,000 hours (i.e. approximately 10 hours a day, including Saturday and Sunday) over a period of about 2½ years, in reading literature, collecting specimens, rearing, maintaining and measuring them, counting samples and drawing figures and, in addition, another 800 hours have been contributed by an assistant who helped to collect, examine and count samples from May to September, 1964. This represents the equivalent of four persons working a normal 40-hour week over a period of one year.

This study is believed to be original in that the systematics of the Forcipomyiinae have hitherto not been examined critically on the basis of systematic principles. The present systematic treatment, in the opinion of the writer, constitutes an important, essential, preliminary step towards further rapid progress in the systematics of the group. The present quantitative ecological study is also original and similarly constitutes a preliminary step towards life-table studies on biting midges and a better understanding of the mechanisms of regulation of insect populations.

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APPENDIX

TABLES

In the following tables, 14 - 31, all measurements were made under high power where 1 unit = 0.00345 mm. except the following which were made under low power where 1 unit = 0.015 mm.

1. <u>LARVA</u>

    Whole Larva
        Body length (L)
        Width (W)
        Depth (D)

2. <u>PUPA</u>

    a) Whole Pupa
        L
        W
        Cph/Abd.

    b) Cephalothorax
        L/W
        Hd/Th
            Dorsal a.
            Ventral a.

3. <u>ADULT</u>

    a) Whole insect
        Body length (L)

    b) Thorax
        L
        W
        CR.

Table 14a.

Proforcipomyia clara n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL*	CALCULATED
WHOLE LARVA	Body length (L) Width(W)/Depth(D)		184 18/19	2.76 mm. 0.95
HEAD	Lateral View	HR (L/D) OH/v qt/ts/sq	75/48 42/24 20/17/37	1.56 1.75 1.18/1/2.18
	Ventral View	L/W tt/ant qq/eyes qq/ss AR (L/W) q (Fil/Tub) s (Fil/Tub) pp/ant	45/45 13/35 15/37 15/44 44/5 15/2 18/2 26/35	1.00 0.37 0.41 0.34 8.80 7.50 9.00 0.74
THORAX	Ant. pseud.	L/W/D	41/29/20	2.05/1.95/1
	Proth. setae	a (Fil/Tub) b (Fil/Tub)	20/5 17/3	4.00 5.67

* The original measurements are given as other ratios and exact calculations can be obtained from these.

Table 14b.

Proforcipomyia clara n. sp. - Measurements of key characters for single male and female pupa.

CHARACTER			Female		Male	
			Original	Calculated	Original	Calculated
WHOLE PUPA	L		134	2.01 mm.	132	1.98 mm.
	W		32	0.48 mm.	31.5	0.47 mm.
	Cph/Abd		51/98	0.52	57/94	0.61
CEPHALO-THORAX	L/W		51/32	1.59	57/31.5	1.81
	Hd/th	Dorsal a.	6.5/36.5	0.18	8/36.5	0.22
		Ventral a.	21/46	0.46	22/49	0.45
	Resp. Horn	L/W	48/25	1.92	43/18	2.39
		TrL/W	35/5	7.00	34/40	8.50
		TrL/HL	35/48	0.73	34/43	0.79
		No. sp. pap. (upper & lower palisades)	22+36	22+36	11+22	11+22
ABDOMEN	3rd segt (L/W/D)		12.5/22/21	0.60/1.05/1	11.5/21/17	0.68/1.24/1
	Last segt (L/W/D)		45/42/34	1.32/1.24/1	36/41/32	1.13/1.28/1
	Term. proc. (L/W/D)		39/20/12	3.25/1.67/1	62/18/15	4.13/1.20/1
	Sex. proc. (L/W/D)		—	—	15/15/6	2.50/2.50/1

Table 14c.

Proforcipomyia clara n. sp. - Measurements of key characters for single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		105	1.58 mm.
HEAD	Prob/Hd		49/67	0.73
	AR		105/103	1.02
	PR		25/6.5	3.85
THORAX	Legs	Fore TR	37.5/35.5	1.06
		Mid TR	25/44.5	0.56
		Hind TR	34/46	0.74
		Tib. spines	.8	8
	Wing	L	64	0.96 mm.
		W	20	0.30 mm.
		CR	28/64	0.44
		vLR	67/64/140	1.05/1/2.19
		rs/r_1	53/38.5	1.38
		RR	14/28	0.50
		M_{3+4}/CU_1	85/35	2.43
ABDOMEN (GENITALIA)	L/W	9th stern.	32/38	0.84
		9th trg.	18/38	0.47
		Bmr	27/16	1.69
		Tmr	20/4.5	4.44
		Aed	14.5/19	0.76
	Clsp	(b/c/b)	11/8/11	1.38/1/1.38

Table 14d.

Proforcipomyia clara n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		88	1.32 mm.
HEAD	Prob/Hd		37/65	0.57
	AR		77/67	1.15
	PR		19/7	2.71
THORAX	Legs	Fore TR	37/22	1.68
		Mid TR	32/25	1.28
		Hind TR	35/30	1.17
		Tib. spines	7	7
	Wing	L	52	0.78 mm.
		W	24	0.36 mm.
		CR	22.5/52	0.43
		vLR	50/45/112	1.11/1/2.49
		rs/r_1	75/40	1.88
		RR	27/21	1.29
		m_{3+4}/Cu_1	75/38	1.97
ABDOMEN	Smaller spmth	L	17	58.65μ
		W	12.5	43.13μ
	Larger spmth	L	20	69.00μ
		W	15	51.75μ

Table 15a.

Proforcipomyia pennielongata n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length		210	3.15 mm.
	Width(W)/Depth(D)		17/17	1.00
HEAD	Lateral View	HR (L/D)	88/55	1.60
		OH/v	47/32	1.47
		pq/tq/pt	21/18.5/40	1.14/1/2.16
	Ventral View	L/W	63/62	1.02
		tt/ant	14/31.5	0.44
		qq/eyes	12/42	0.29
		qq/ss	12/43	0.28
		AR (L/W)	58/13	4.46
		q (Fil/Tub)	17/3	5.67
		s (Fil/Tub)	24/1.5	16.00
		pp/ant	33/31.5	1.05
THORAX	Ant. pseud.	L/W/D	55/34/40	1.62/1/1.18
	Proth. setae	a (Fil/Tub)	26/4	6.50
		b (Fil/Tub)	21/2	10.50

Table 15b.

Proforcipomyia pennielongata n. sp. - Measurements of key characters for one female and three male pupae.

Character			Female		Male			
			Original	Calculated	1	2	3	$\bar{x}$
WHOLE PUPA	L		172	2.58 mm.	175	179	177	2.66 mm.
	W		40	0.60 mm.	42	42	42	0.63 mm.
	Cph/Abd		64/133	0.48	70/134	74/134	73/134	0.54
CEPHALO-THORAX	L/W		64/40	1.60	70/42	74/42	73/42	1.72
	Hd/th	Dorsal a	5/46	0.11	6/47	7/49	8/49	0.15
		Ventral a	21/60	0.35	26/64	26/66	25/65	0.40
	Resp. Horn	L/W	55/35	1.57	53/36	55/34	55/34	1.57
		TrL/W	42.5/6	7.08	39.5/6	40/6	40/6	6.64
		TrL/HL	42.5/55	0.77	39.5/53	40/55	40/55	0.73
		No. sp. pap. (upper & lower palisades)	22+36	22+36	23+42	23+38	23+38	23+39
ABDOMEN	3rd segt (L/W/D)		15/26.5/24	1/1.77/1.60	14.5/25/25	14/26/26	15/26.5/24	1/1.78/1.73
	Last segt (L/W/D)		60/54/45	1.33/1.20/1	51.5/52/48	58/53/44	57/53/44	1.22/1.16/1
	Term. proc. (L/W/D)		67/24/16	4.19/1.50/1	93/23/19	95/25/18	95/24.5/20	4.97/1.28/1
	Sex. proc. (L/W/D)		—	—	19/18/6	19/20/7.5	19/19/6	2.96/2.95/1

$\bar{x}$ = mean $\left(\frac{\sum x}{n} \right)$

Table 15c.

Proforcipomyia pennielongata n. sp. - Measurements of key characters for single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		120	1.80 mm.
HEAD	Prob/Hd		53.5/74	0.72
	AR		112/123	0.92
	PR		28/6	4.67
THORAX	Legs	Fore TR	44/40	1.10
		Mid TR	22.5/51	0.44
		Hind TR	41/56	0.73
		Tib. spines	7	7
	Wing	L	72	1.08 mm.
		W	23	0.35 mm.
		CR	30/72	0.42
		vLR	75/70/156	1.07/1/2.23
		rs/r_1	61/40	1.53
		RR	14/34	0.41
		m_{3+4}/Cu_1	99/41	2.42
ABDOMEN (GENTALIA)	L/W	9th stern.	23/40	0.58
		9th trg.	30/40	0.75
		Bmr	37/21	1.76
		Tmr	28/5	5.60
		Aed	29/19	1.53
	Clsp	(b/c/b)	15/5/15	3.00/1/3.00

Table 15d.

Proforcipomyia pennielongata n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
HEAD	AR		142/129	1.10
	PR		40/10.5	3.81
	Palpal segts.		12:13:40:21:13	-
THORAX	Leg	Hind TR	72/72	1.00
	Wing	L	94	1.02 mm.
		W	39	0.42 mm.
		CR	50/94	0.53
		vLR	22.5/20/45	1.13/1/2.25
		rs/r_1	28.5/18	1.58
		RR	7.5/15	0.50
		m_{3+4}/Cu_1	31/16	1.94
ABDOMEN	Smaller spmth	L	25.5	54.26μ
		W	20	42.55μ
	Larger spmth	L	32	68.09μ
		W	27	57.23μ

Table 16a.

Forcipomyia (*Forcipomyia*) *bikanni* n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length (L)		280	4.20 mm.
	Width(W)/Depth(D)		34.5/34.5	1.00
HEAD	Lateral View	HR (L/D)	144/95	1.52
		OH/v	68/61	1.12
		qt/ts/sq	40/57/38	1.05/1.50/1
	Ventral View	L/W	95/105	0.48
		tt/ant	34/70	0.49
		qq/eyes	21/89	0.24
		qq/ss	21/96	0.22
		AR (L/W)	43/18	2.39
		q (Fil/Tub)	38/5	7.60
		s (Fil/Tub)	40/2	20.00
		Eye (Ht/W)	3/10	0.30
THORAX	Ant. pseud.	L/W/D	73/88/35	2.09/2.51/1
	Proth. setae	a (Fil/Tub)	39/4	9.75
		b (Fil/Tub)	65/3	21.67

Table 16b.

Forcipomyia (*Forcipomyia*) *bikanni* n. sp. - Measurements of key characters for single male and female pupa.

CHARACTER			Female		Male	
			Original	Calculated	Original	Calculated
WHOLE PUPA	L		145	2.18 mm.	220	3.30 mm.
	W		68	1.02 mm.	69	1.04 mm.
	Cph/Abd		119/177	0.67	97/155	0.63
CEPHALO-THORAX	L/W		119/68	1.75	97/68	1.43
	Hd/th	Dorsal a	23/65	0.35	18/62	0.29
		Ventral a	64/108	0.59	40/84	0.48
	Resp. Horn	L/W	73/30	2.43	69/29	2.38
		TrL/W	73/10	7.30	69/10	6.90
		TrL/HL	73/73	1.00	69/69	1.00
		No. sp. pap.	18	18	20	20
ABDOMEN	3rd segt (L/W/D)		28/50/58	1/1.79/2.07	20/44/35	1/2.20/1.75
	Last segt (L/W/D)		14/21/22	0.67/1/1.05	—	—
	Term. proc. (L/W/D)		25/12/12	2.08/1/1.00	73/23/30	3.17/1/1.30
	Sex. proc. (L/W/D)		—	—	16/20/12	1.33/1.67/1

Table 16c.

Forcipomyia (*Forcipomyia*) *bikanni* n. sp. - Measurements of key characters for four adult males.

CHARACTER			1	2	3	4	$\bar{x}$
WHOLE INSECT	Body length (L)		125	141	145	135	2.04 mm.
HEAD	Prob/Hd		60/105	49/100	54/90	56/90	0.57
	AR		109/109	115/117	126/117	112/115	1.01
	PR		24.5/8	27/8	28/8	26/8	3.30
THORAX	Legs	Fore TR	29/35	41/41	43/40	38/40	0.96
		Mid TR	35/45	37/51	39.5/52	36/50	0.75
		Hind TR	40/54	40/56	41/61	39/56	0.71
		Tib. spines	8	9	8	9	8.50
	Wing	L	62	66	71	65	0.99 mm.
		W	21	24	24	23	0.35 mm.
		CR	26.5/62	28/66	30.5/71	28/65	0.43
		vLR	80/70/130	87/77/143	89/80/151	82/70/137	1.13/1/1.89
		rs/r_1	40/25	40/22	46/33	43/28	1.59
		RR	18/15	14/18	17/20	15/18	0.92
		m_{3+4}/Cu_1	91/46	100/48	100/50	96/47	2.03
ABDOMEN (GENITALIA)	L/W	9th stern.	26/48	22/50	20/50	21/50	0.45
		9th trg.	33/48	31/50	30/50	28/50	0.62
		Bmr	41/21	44/21	43/23	40/20	1.98
		Tmr	33/6	35.5/6	33/6	35/6.5	5.58
		Aed	20/31	20/29	20/30	22/33	0.67

TABLE 16d

Forcipomyia (*Forcipomyia*) *bikanni* n.sp. - Measurement of key characters for 10 adult females

CHARACTER		SPECIMEN NO.										$\bar{x}$
		1	2	3	4	5	6	7	8	9	10	
WHOLE INSECT	Body length (L)	120	136	134	150	123	128	142	115	133	117	1.99mm.
HEAD	Prob/Hd.	70/89	51/87	51/87	55/83	46/80	45/80	49/85	45/85	48/86	47/84	0.59
	AR	75/109	83/104	65/96	82/118	63/100	75/122	74/100	63/95	73/105	70/102	0.69
	PR	27/10	25/11	25/10	27/10	22.5/9	28/10.5	28/10	25/10	25/9	25/9	2.63
THORAX	LEGS Fore TR	43/35	43/34	43/35	49/40	42/33	46/37	48/36	43/34	43/34	42/32	1.26
	Mid TR	44/48	46/49	40/43	44/50	40/42.5	46/49	46/48	42/44	41/44	40/42	0.94
	Hind TR	48/56	48/61	43/53	49/55	44/51	49/55.5	50/56	40/50	46/53	44/51	0.85
	Tib. spines	8	8	8	9	8	8	10	8	8	9	8.40
	WING L	71.5	55	65	72	62.5	69	70	65	64	65	0.99mm.
	W	31.5	26	29	33	27	31	31	29	28	29	0.43mm.
	CR	33/71.5	25/55	30/65	33/72	28/62.5	32/69	31/70	30/65	28/64	31/65	0.46
	vLR	88/73/145	25/22.5/39	82/68/133	85/75/140	78/68/132	81/70/138	82/75/140	78/70/128	78/70/120	81/72/128	1.14/1/1.86
	rs/r_1	55/36	17/11.5	50/32	64/39	50/30	60/40	52/34	55/36	48/30	58/38	1.56
	RR	25/22	7/6.5	17/22	27/24	21/17.5	28/22	20/23	21/23.5	23/20	19/27	1.02
	m_{3+4}/cu_1	113/64	37.5/20	104/60	125/68	100.56	110/60	112/64	112/59	110/60	113/62	1.81
ABDOMEN	Smaller Spmth. L	28	28	27	34	29	30	28	24	27	30	98.33 μ
	W	21.5	22	20	20	19	20	20	18	18	20	68.48 μ
	Larger Spmth. L	36	38	36	42	36	43	41	34	40	42	133.86 μ
	W	25	26	23.5	28	25	27	27	22	26	26	88.15 μ

TABLE 17a

Forcipomyia (*Forcipomyia*) *bipunctatapropinqua* n.sp - Measurements of key characters for 10 fourth-instar larvae

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE LARVA		Body length(L)	250	272	300	280	318	254	300	305	275	283	4.26mm.	0.33mm.	0.11mm.
		Width(W)/Depth(D)	28/30	29/29	32/30	37/33	35/33	32/31	36/34	37/35	37.5/35	33/31	1.05	0.05	0.02
HEAD	Lateral View	HR(L/D)	138/84	141/85	146/87	146/87	155/89	140/82	154/88	153/88	150/85	145/85	1.71	0.04	0.01
		OH/V	65/54	62/35	71/58	68/60	71/61	70/54	71/61	72/61	69/60	68/56	1.19	0.05	0.02
		qt/ts/sq	38/43/18.5	39/40/23	42/45/22	43/43/26	41/47/24	39/40/22	41/43/25	39/45/26	42/47/24	40/46/23	1.74/1.90/1	0.15/0.20/1	0.05/0.06/0.32
	Ventral View	L/W	82/81	83/83	91/90	91.5/89	89/93	86/90	90/94	92/98	84/91	87/90	0.98	0.05	0.02
		tt/ant	27/64	28/65	31/65	30/65	31/64	28/60	31/66	31/66	30/65	29/64	0.46	0.02	0.01
		qq/eyes	19/75	20/75	18/81	20.5/81	20/79	18/78	21/80	21/84	20/79	18/78	0.25	0.02	0.01
		qq/ss	19/75	20/78	78/80	20.5/86	20/84	18/81	21/85	21/88	20/83	18/83	0.24	0.01	0.004
		AR(L/W)	36/14	35/13.5	36/13	36/14	37/14	24/12	37/14	36/12	35/14	36/14	2.59	0.25	0.08
		'q'(Fil/Tub)	34/4	33/4	33/4	34/4	34/4	34/4	39/4	31/4	33/4	43/4	8.70	0.88	0.28
		's'(Fil/Tub)	17/1.5	17/1.5	19/1.5	16/1.2	18/1.5	17/1.5	21/2	17/1.5	19/1.5	21/1.5	12.05	1.09	0.34
		Eye(Ht/W)	4/9	3/8	3/8	2.5/9	2.5/8	2/8	3.5/10	2/8	2.5/9	2.3/8	0.32	0.06	0.02
THORAX	Ant. pseud.	L/W/D	73/47/25	81/56/40	73/55/28	73/55/30	85/57/32	72/55/27	86/55/32	80/58/30	75/55/28	84/55/30	2.61/1.83/1	0.24/0.18/1	0.08/0.06/0.32
	Proth. setae	a(Fil/Tub)	34/4	32/4	34/4	32/4	35/4.2	32/4	34/4	36/4	31/4.5	35/4	8.22	0.57	0.18
		b(Fil/Tub)	65/5	68/5	61/5	65/5	65/5	60/4.5	67/5.5	67/5.5	65/5	68/5.2	12.89	0.48	0.15

σ = standard deviation $\left(\sqrt{\frac{\Sigma x^2 - \frac{(\Sigma x)^2}{n}}{n-1}}\right)$

$S_{\bar{x}}$ = standard error $\left(\frac{\sigma}{\sqrt{n}}\right)$

[redacted]

TABLE 17b

Forcipomyia (*Forcipomyia*) *bipunctatapropinqua* n.sp. - Measurements of key characters for 10 male pupae

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE PUPA	L		165	169	172	145	170	173	172	180	149	155	2.48mm.	0.17mm.	0.05mm.
	W		47	41	40	38	40	42	41	45	36	37	0.61mm.	0.05mm.	0.02mm.
	Cph/Abd.		81/114	75/113	75/112	69/104	70/120	75/126	73/126	88/124	65/94	67/119	0.64	0.06	0.02
CEPHALOTHORAX	L/W		81/47	75/41	75/40	69/38	70/40	75/42	73/41	88/45	65/36	67/37	1.81	0.07	0.02
	Hd/Th.	Dorsal a.	12/46	12/45	12/48	11/40	12/42	12/47	10/47	16/52	11/40	12/41	0.27	0.03	0.01
		Ventral a.	31/71	28/62	25/63	24/59	25/62	27/57	27/63	29/66	23/52	25/58	0.43	0.03	0.01
	Resp. Horn	L/W	40/18	39/18	40/18	40/16	35/16	40/18.5	40/17	54/22	36/15	35/15	2.30	0.13	0.04
		TrL/W	40/3.5	39/3.5	40/3.5	39/3	34/3	39/4	40/3.5	54/5	35/3	32/2.9	11.38	0.82	0.26
		TrL/HL	40/40	39/39	40/40	39/40	34/35	39/40	40/40	54/54	35/36	32/35	0.98	0.03	0.01
		No sp.pap.	26		17	25	18	24	24	29	19	19	22.33	8.09	2.56
ABDOMEN	3rd sgt.(L/W/D)		15/21/25	14/26/25	15/28/24	13/25/22	15/23/23	16/29/25	15/25/25	15/31/27	12/24/25	16/28/27	1/1.79/1.75	1/0.21/0.19	0.32/0.07/0.06
	Sex.proc.(L/W)		18/18	18/21	20/21	17/20	17/19	19/22	16/20	21/21	15/20	14/21	0.86	0.11	0.03
	Term.proc.(L/W/D)		82/22/28	79/22/24	75/22/21	71/22/24	70/22/23	75/25/24	69/22/23	75/22/24	66/19/21	66/21/21	3.33/1/1.07	0.23/1/0.09	0,72/0.52/0.03

TABLE 17c

Forcipomyia (*Forcipomyia*) *bipunctatapropinqua* n.sp. - Measurements of key characters for 10 female pupae

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1.	2	3	4	5	6	7	8	9	10			
WHOLE PUPA		L	160	148	164	160	164	163	150	153	118	147	2.29mm.	0.21mm.	0.07mm.
		W	39	40	39	39	39	42	35	39	35	35	0.57mm.	0.04mm.	0.01mm.
		Cph./Abd.	69/109	70/108	69/115	65/110	68/112	66/113	61/105	65/106	57/18	64/108	0.61	0.03	0.01
CEPHALO-THORAX		L/W	69/39	70/40	69/39	65/34	68/39	66/42	61/35	65/39	57/35	64/35	1.71	0.08	0.02
	Hd/Th.	Dorsal a.	12/41	10/42	10/42	9/40	11/40	8.5/44	9/42	9/42	8/37	9/39	0.23	0.03	0.01
		Ventral a.	27/58	25/61	26/60	24/56	25/56	26/59	28/56	25/58	24/50	25/58	0.45	0.03	0.01
	Resp. Horn	L/W	39/16	39/18.5	44/18	37/17	36/16.5	33/16	36/18	37/18	33/17	31/15.5	2.14	0.19	0.06
		TrL/W	40/3	39/4	44/3.5	37/3	35/3.5	35/4	36/3.5	36/3	33/3	31/3	11.04	1.46	0.46
		TrL/HL	40/39	39/39	44/44	37/37	35/36	35/33	36/35	36/37	33/33	31/31	1.00	0.03	0.01
		No.sp.pap.	19	21	23	19	17	21	23	21	20	21	20.50	1.84	0.58
ABDOMEN		3rd segt.(L/W/D)	16/27/25	15/28/25	15.5/26/25	15/28/24	16/30/25	15/28/27	15/27/24	16/27.5/27	12/24/20	14/26/26	1/1.82/1.66	1/0.10/0.03	0.32/0.03/0.01
		Last segt.(L/W/D)	45/49/48	44/49/50	45/50/53	46/51/50	47/54/49	52/52/52	47/52/52	44/51/51	48/50/50	-	1/1.10/1.09	1/0.35/0.35	0.32/0.11/0.11
		Term.proc.(L/W)	53/20/24	52/22/25	45/22/22	43/22/20	51/22/20	44/22/19	50/20/25	39/23/22	48/22/21	-	2.19/1/1.02	0.75/1/0.35	0.24/0.32/0.11

TABLE 17d

Forcipomyia (*Forcipomyia*) *bipunctatapropinqua* n.sp. - Measurements of key characters for 10 adult males

CHARACTER		SPECIMEN NO. 1	2	3	4	5	6	7	8	9	10	$\bar{x}$	σ	$S_{\bar{x}}$
WHOLE INSECT	Body length(L)	162	141	147	164	173	164	170	189	155	175	2.46mm.	0.21mm.	0.07mm.
HEAD	Prob/Hd.	70/105	60.5/99	62/93	68/99	75/103	67/100	64/90	75/100	60/100	68/97	0.67	0.04	0.01
	AR	144/122	118/110	123/108	126/117	132/123	116/117	116/115	140/117	128/113	137/120	1.10	0.07	0.02
	PR	30/8.5	26/7.5	27/8	27/8	28/9	26/8.5	27/8.5	30/9	27/8	27/8	3.32	0.15	0.05
THORAX	LEGS Fore TR	52/42	50/38	48/37	47/37	50/40	52/40	48/37	55/42	46/37	56/42	1.29	0.03	0.01
	Mid TR	48/52	46/47	47/45	47/46	48/47	49/51	44/45	53/53	46/46	56/50	1.01	0.05	0.02
	Hind TR	58/60.5	53/52	55/50	55/55	54/55	55/55	51/55	58/59	50/52	58/56	1.00	0.05	0.02
	Tib. spines	9	9	9	9	10	9	9	9	9	9	9.10	0.32	0.10
	WING L	84	75	75	81	78	78	75.5	82	75	85	1.18mm.	0.06mm.	0.02mm.
	W	30	25	27	28	27	27	27.5	29	23	29	0.41 mm.	0.03mm.	0.01mm.
	CR	35/84	33/75	30/75	35.5/81	34/78	34/78	32/75.5	34/82	33/75	35/85	0.43	0.01	0.004
	VLR	113/97/175	91/81/154	95/85/160	103/96/171	100/94/170	101/91/165	97/87/156	112/103/173	100/90/165	106/95/182	1.11/1/1.82	0.04/1/0.07	0.01/0.32/0.02
	rs/r_1	50/27	52/35	48/28	52/30	48/29	50/33	50/30	48/29	47/30	51/34	1.63	0.12	0.04
	RR	19/18	20/21	18/18	20/20	19/19	18/20	17/18	16/17	15.5/22	19/19	0.95	0.10	0.03
	m_{3+4}/cu_1	131/60	114/54	112/53	119/56	112/52	114/55	114/57	138/62	108/45	125/55	2.17	0.11	0.04
ABDOMEN (GENI-TALIA)	9th stern	24/54	23/51	22/45	22/51.5	23/47	23/51	21/47	22/52	22/46	24/52	0.46	0.03	0.01
	9th **terg.**	22/54	25/51	23/45	22/51.5	27/47	22/51	28/47	25/52	18/46	25/52	0.48	0.07	0.02
	Bmr	46/21	45/21	45/19	45/21	47/21	45/21	45/20	45/20	41/19	46/21	2.21	0.07	0.02
	Tmr	37/7	35/6.2	35/6	36/7	38/7	36/6.5	36/6	38/7	35/7	38/7	5.47	0.31	0.10
	Aed.	12/29	18.5/30	19/25	14/29	20/26	21/26	20/28	20/30	20/29	24/30	0.67	0.13	0.04
	Clsp (b/c/b)	19/11.5/18.5	18/9/18	18/6/17	20/10/20	18/10/18	19/10/19	18/10/18	18/10/18	17/9/18	20/9/19	2.01/1/1.99	0.38/1/0.33	0.12/0.32/0.11

TABLE 17e

Forcipomyia (*Forcipomyia*) *bipunctatapropinqua* n.sp. - Measurements of key characters for 10 adult females

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE INSECT	Body length(L)		130	140	152	149	150	145	140	148	134	125	2.12mm.	0.14mm.	0.04mm.
HEAD	Prob/Hd.		58/84	64/80	81/90	70/87	80/96	70/93	65/86	66/82	68/87	62/80	0.79	0.06	0.02
	AR		73/100	78/104	84/113	74/109	90/116	74/101	77/104	78/106	78/105	71/97	0.74	0.02	0.01
	PR		25/10	26/11	27/10.5	25/10	28/11	23/10	23/9.5	24/10	24/10.5	25/9.5	2.45	0.12	0.04
THORAX	LEGS	Fore TR	43/31	43/31	50/35.5	45/31	51/35	44/30	43/30	50/34	47/32	41/27	1.45	0.05	0.01
		Mid TR	44/41	43/40	52/46.5	47/40	54/47	45/38.5	46/39	47/39	49/40	42/32	1.17	0.08	0.02
		Hind TR	50/47	50/47	58/54	54/48	59/35	51/47	51/47	52/46	56/49	45/37	1.11	0.05	0.02
		Tib.spines	8	8	8	9	8	8	8	8	9	8	8.20	0.42	0.13
	WING	L	66	69	74	73	82	71	68	76	71	65	1.07mm.	0.08mm.	0.02mm.
		W	30	30	33	30	36	31	31	31	31	27	0.47mm.	0.04mm.	0.01mm.
		VLR	82/70/130	98/69/129	85/74/151	88/77/140	100/88/142	80/70/126	78/66/126	85/72/136	86/73/136	74/64/130	1.16/1/1.87	0.02/1/0.12	0.01/0.32/0.04
		CR	31/66	31/69	33/74	32/73	33/82	31/71	29/68	30.5/76	31/71	29/65	0.44	0.02	0.01
		rs/r_1	60/40	59/40	65/45	59/35	69/46	60/40	54/33	51/32	55/34	54/37	1.54	0.08	0.03
		RR	23/22	22/22	23/27	17/20	23/26	20/26	20/18	24/18	25/19	21/20	1.02	0.19	0.06
		m_{3+4}/cu_1	118/66	115/65	126/66	120/63	138/70	119/63	104/60	114/60	110/61	103/45	1.90	0.15	0.05
ABDOMEN	Smaller Spmth.	L	20	18	21	24	25	23	21	23	21	18	73.83 μ	8.16 μ	2.58 μ
		W	13	12	14	13	12.5	14	11	14	13	12	44.51 μ	3.43 μ	1.09 μ
	Larger Spmth.	L	24	21	25	25	26.5	24	21.5	24	21	20	80.04 μ	7.46 μ	2.36 μ
		W	13	12.5	13	14	12	13	12	13.5	13	13	44.51 μ	2.12 μ	0.67 μ

Table 18a.

Forcipomyia (*Forcipomyia*) *intonsa* n. sp. - Measurements of key characters for single third-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length (L)		174	2.61 mm.
	Width(W)/Depth(D)		25/21	1.19
HEAD	Lateral View	HR (L/D)	123/80	1.54
		OH/v	60/49	1.23
		qt/ts/sq	33/41/24	1.38/1.71/1
	Ventral View	L/W	75/85	0.88
		tt/ant	26/58	0.45
		qq/eyes	21/76	0.28
		qq/ss	21/77.5	0.27
		AR (L/W)	38/15	2.53
		q (Fil/Tub)	50/3	16.67
		s (Fil/Tub)	65/2	32.50
		Eye (Ht/W)	5/10	0.50
THORAX	Ant. pseud.	L/W/D	90/49/57	1.58/0.86/1
	Proth. setae	a (Fil/Tub)	18/3	6.00
		b (Fil/Tub)	68/7	9.71

Table 18b.

Forcipomyia (*Forcipomyia*) *intonsa* n. sp. - Measurements of key characters for one female and three male pupae.

CHARACTER			Female		Male			
			Original	Calculated	1	2	3	$\bar{x}$
WHOLE PUPA	L		204	3.06 mm.	200	210	206	3.03 mm.
	W		50	0.75 mm.	52	49	50	0.76 mm.
	Cph/Abd		101/141	0.72	99/136	99/144	98/145	0.70
CEPHALO-THORAX	L/W		101/50	2.02	99/52	99/49	98/50	1.96
	Hd/th	Dorsal a.	14/70	0.20	13/56	13/58	14/65	0.22
		Ventral a.	31/90	0.34	30/88	30/83	30/87	0.35
	Resp. Horn	L/W	30/13	2.31	32/12	30/11.5	29/12	2.56
		TrL/W	25/6	4.17	27/5	25/5	25/5	5.13
		TrL/HL	25/30	0.83	27/32	25/30	25/29	0.85
		No. sp. pap.	22	22	21	21	21	21
ABDOMEN	3rd segt (L/W/D)		19/35/33	1/1.84/1.74	20/35/31	18/33/30	16/32/33	1/1.86/1.76
	Last segt (L/W/D)		59/63/66	0.94/1/1.05	—	—	—	—
	Term. proc. (L/W/D)		105/25/36	4.20/1/1.44	124/24/29	135/26/30	120/24/32	5.12/1/1.23
	Sex. proc. (L/W/D)		—	—	40/13/13	45/13/13	45/14/14	3.25/1.00/1

Table 18c.

Forcipomyia (*Forcipomyia*) *intonsa* n. sp. - Measurements of key characters for single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		172	2.59 mm.
HEAD	Prob/Hd AR PR		95/100 161/135 35/9	0.95 1.19 3.89
THORAX	Legs	Fore TR Mid TR Hind TR Tib. spines	40/71 31/91 38/96 9	0.56 0.34 0.40 9
	Wing	L W CR vLR rs/r_1 RR m_{3+4}/Cu_1	94.5 29 44/94.5 127/117/182 68/46 24/35 155/64	1.42 mm. 0.44 mm. 0.47 1.09/1/1.56 1.48 0.69 2.42
ABDOMEN (GENITALIA)	L/W	9th stern. 9th trg. Bmr Tmr Aed	26/56 30/56 45/21.5 38/7 23/20	0.46 0.54 2.09 5.43 1.15
	Clsp	(b/c/b)	20/7/20	2.86/1/2.86

Table 18d.

Forcipomyia (*Forcipomyia*) *intonsa* n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		225.5	2.45 mm.
HEAD	AR		251/165	1.52
	PR		39/12.5	3.11
THORAX	Legs	Fore TR	38/54	0.70
		Mid TR	31/70	0.44
		Hind TR	35.5/68	0.52
		Tib. spines	7	7
	Wing	L	129	1.40 mm.
		W	51.5	0.56 mm.
		CR	69.5/129	0.54
		rs/r_1	156/75	2.08
		RR	67/35	1.91
		m_{3+4}/Cu_1	41/20.5	2.00
		vLR	31/27/50	1.15/1/1.85
ABDOMEN	Smaller spmth	L	21	72.41µ
		W	16	55.17µ
	Larger spmth	L	23	79.31µ
		W	16	55.17µ

Table 19a.

Forcipomyia (*Forcipomyia*) *swezeyanaadfinis* n. sp. - Measurements of key characters for one third and one fourth-instar larva.

CHARACTER			3rd-instar		4th-instar	
			Original	Calculated	Original	Calculated
WHOLE LARVA	Body length (L)		135	2.02 mm.	172	2.58 mm.
	Width(W)/Depth(D)		17/15	1.13	18/17	1.06
HEAD	Lateral View	HR (L/D)	75/45	1.67	103/56	1.84
		OH/v	35/34	1.29	47/45	1.04
		qt/ts/sq	11/19/15.5	1/1.73/1.41	12/26/20	1/2.17/1.67
		pq/qs/sp	29/16/21	1.81/1/1.31	41/20/28	2.05/1/1.40
	Ventral View	L/W	48/47	1.02	70/68	1.03
		tt/ant	16/31	0.52	21/37	0.57
		qq/eyes	9/34	0.26	13/48	0.27
		qq/ss	9/41	0.22	13/57	0.23
		AR (L/W)	13/6	2.17	17/9	1.89
		q (Fil/Tub)	24/2	12.00	21/2	10.50
		s (Fil/Tub)	22/1.1	20.00	42/2	21.00
		Eye (Ht/W)	—	—	6/1	6.00
THORAX	Ant. pseud.	L/W/D	40/35/35	1.14/1/1.00	50/40/30	1.67/1.33/1
	Proth. setae	*a* (Fil/Tub)	18/2	9.00	27/2.5	10.76
		b (Fil/Tub)	30/5	6.00	47/5	9.40

Table 19b.

Forcipomyia (*Forcipomyia*) *swezeyanaadfinis* n. sp. - Measurements of key characters for two male pupae.

CHARACTER			1	2	x̄
WHOLE PUPA	L		163	160	2.42 mm.
	W		37	40	0.58 mm.
	Cph/Abd		73/113	72/113	0.64 mm.
CEPHALO-THORAX	L/W		73/37	72/40	1.89
	Hd/th	Dorsal a.	10/48	10/47	0.21
		Ventral a.	25/68	25/67	0.37
	Resp. Horn	L/W	26/13	25/13	1.96
		TrL/W	21/5	20/5	4.10
		TrL/HL	21/26	20/25	0.80
		No. sp. pap.	12	13	12.50
ABDOMEN	3rd segt.(L/W/D)		16/27/24	16/29/24	1/1.75/1.50
	Term. proc. (L/W/D)		75/18/22	77/18/22	4.22/1/1.22
	Sex. proc. (L/W/D)		10/16/9	12/15/9	1.22/1.72/1

Table 19c.

Forcipomyia (Forcipomyia) swezeyanaadfinis n. sp. - Measurements of key characters for single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		125	1.88 mm.
HEAD	Prob/Hd		53/100	0.53
	AR		107/105	1.02
	PR		21/7.5	2.80
THORAX	Legs	Fore TR	37/31	1.19
		Mid TR	30/42	0.71
		Hind TR	33/49	0.67
		Tib. spines	8	8
	Wing	L	60	0.90 mm.
		W	30	0.45 mm.
		CR	24.5/60	0.41
		vLR	73/62/124	1.18/1/2.00
		rs/r_1	37/23	1.61
		RR	13/14	0.93
		m_{3+4}/Cu_1	90/40	2.25
ABDOMEN (GENITALIA)	L/W	9th stern.	18/50	0.36
		9th trg.	20/50	0.40
		Bmr	35/16.5	2.12
		Tmr	29/5	5.80
		Aed	22/17	1.29
	Clsp	(b/c/b)	17/6/17	2.83/1/2.83

Table 19d.

Forcipomyia (*Forcipomyia*) *swezeyanaadfinis* n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		113	1.70 mm.
HEAD	Prob/Hd		53/75	0.71
	AR		70/85	0.82
	PR		19/10	1.90
THORAX	Legs	Fore TR	35/26	1.35
		Mid TR	32/35	0.92
		Hind TR	37/41	0.90
		Tib. spines	8	8
	Wing	L	52.5	0.79 mm.
		W	23	0.35 mm.
		CR	22/52.5	0.42
		rs/r_1	45/29	1.55
		RR	13/20	0.65
		m_{3+4}/Cu_1	85/43	1.98
		vLR	60/50/100	1.20/1/2.00
ABDOMEN	Smaller spmth	L	12	41.4µ
		W	9	31.05µ
	Larger spmth	L	14	48.30µ
		W	9	31.05µ

Table 20a.

Forcipomyia (*Forcipomyia*) *securis* n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		229	3.44 mm.
	Width(W)/Depth(D)		27/27	1.00
HEAD	Lateral View	HR (L/D)	125/71	1.76
		OH/v	60/43	1.40
		qt/ts/sq	30.5/38/19	1.61/2.00/1
	Ventral View	L/W	65/77	0.84
		tt/ant	22/50	0.44
		qq/eyes	17.5/68	0.26
		qq/ss	17.5/70	0.25
		AR (L/W)	31/10	3.10
		q (Fil/Tub)	27/3	9.00
		s (Fil/Tub)	17/1.5	11.33
		Eye (Ht/W)	2/7	0.29
THORAX	Ant. pseud.	L/W/D	75/44/60	1.25/0.73/1
	Proth. setae	*a* (Fil/Tub)	26/5	5.20
		b (Fil/Tub)	40/7	5.71

Table 20b.

Forcipomyia (Forcipomyia) securis n. sp. - Measurements of key characters for one female and two male pupae.

CHARACTER			Female		Male		
			Original	Calculated	1	2	$\bar{x}$
WHOLE PUPA	L		160	2.40 mm.	161	170	2.48 mm.
	W		47	0.71 mm.	48	44	0.69 mm.
	Cph/Abd		72/113	0.64	76/112	80/118	0.68
CEPHALO-THORAX	L/W		72/47	1.53	76/48	80/44	1.70
	Hd/th	Dorsal a	10/50	0.20	10/54	11/52	0.20
		Ventral a	30/69	0.44	31/67	30/69	0.45
	Resp. Horn	L/W	47/15	3.13	46/12	48/14	3.63
		TrL/W	41/3.5	11.71	39/4	42/4	10.13
		TrL/HL	41/47	0.87	39/46	42/48	0.86
		No. sp. pap.	17	17	17	18	17.50
ABDOMEN	3rd segt (L/W/D)		12/32/30	0.40/1.07/1	15/30/26	15/29/26	0.58/1.13/1
	Last segt (L/W/D)		41/20/50	2.05/1/2.50	76/21/24	77/21/22	3.33/0.92/1
	Term. proc.)L/W/D)		48/54/25	1.92/2.16/1	—	—	—
	Sex. proc. (L/W/D)		—	—	15/16/15	15/18/14	1.04/1.18/1

Table 20c.

Forcipomyia (Forcipomyia) securis n. sp. - Measurements of key characters for single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		118	1.77 mm.
HEAD	Prob/Hd		65/78	0.83
	AR		119/103	1.16
	PR		25/8	3.13
THORAX	Legs	Fore TR	37/37	1.00
		Mid TR	30/48	0.63
		Hind TR	37/53	0.70
		Tib. spines	9	9
	Wing	L	65.2	0.98 mm.
		W	22	0.33 mm.
		CR	26.2/65.2	0.40
		vLR	78/71/135	1.10/1/1.90
		rs/r_1	41/28	1.46
		RR	18/14	1.29
		m_{3+4}/Cu_1	102/44	2.32
ABDOMEN (GENITALIA)	L/W	9th stern.	20/39	0.51
		9th trg.	30/39	0.77
		Bmr	41/16	2.56
		Tmr	28/4.5	6.22
		Aed	20/25	0.80
	Clsp	(b/c/b)	15/10/15	1.50/1/1.50

Table 20d.

Forcipomyia (*Forcipomyia*) *securis* n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		99	1.49 mm.
HEAD	Prob/Hd		54/76	0.71
	AR		55/107	0.51
	PR		21/9	2.33
	Legs	Fore TR	35/31	1.13
		Mid TR	31/41	0.76
		Hind TR	39/49	0.80
		Tib. spines	8	8
THORAX	Wing	L	54	0.81 mm.
		W	24	0.36 mm.
		CR	22/54	0.41
		vLR	55/45/105	1.22/1/2.33
		rs/r_1	40/25	1.60
		RR	17/13.5	1.26
		m_{3+4}/Cu_1	78/40	1.95
ABDOMEN	Smaller spmth	L	18	62.10µ
		W	16	55.20µ
	Larger spmth	L	20	69.00µ
		W	17	58.65µ

Table 21a.

Forcipomyia (*Schizoforcipomyia lerouxi* n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length (L)		196	2.94 mm.
	Width(W)/Depth(D)		24/22	1.09
HEAD	Lateral View	HR (L/D)	120/75	1.60
		OH/v	53/54	0.98
		qt/tu/uq	35/22/37	1.59/1/1.68
	Ventral View	L/W	63/75	0.84
		tt/ant	24/46	0.52
		qq/eyes	19/55	0.35
		qq/pp	19/38	0.50
		AR (L/W)	35/9	3.89
		q (Fil/Tub)	81/2	40.50
		u (Fil/Tub)	50/2	25.00
		Eye (Ht/W)	3/6	0.50
THORAX	Ant. pseud.	L/W/D	85/65/38	2.24/1.71/1
	Proth. setae	*a* (Fil/Tub)	27/7	3.86
		b (Fil/Tub)	100/5	20.00

Table 21b.

Forcipomyia (*Schizoforcipomyia*) *lerouxi* n. sp. - Measurements of key characters for two female pupae.

CHARACTER			1	2	$\bar{x}$
WHOLE PUPA	L		158	159	2.38 mm.
	W		43	42	0.64 mm.
	Cph/Abd		73/118	72/114	0.63
CEPHALO-THORAX	L/W		73/43	72/42	1.71
	Hd/th	Dorsal a.	8/47	7/44	0.17
		Ventral a.	24/57	25/62	0.41
	Resp. Horn	L/W	20/10	23/10	2.15
		TrL/W	15/4	19/4	4.25
		TrL/HL	15/20	19/23	0.79
		No. sp. pap.	11	11	11
ABDOMEN	3rd segt (L/W/D)		15/30/26	14/28/26	1/2.00/1.80
	Last segt (L/W/D)		40/57/55	44/55/50	0.75/1/0.94
	Term. proc. (L/W/D)		66/19/19	65/19/19	3.45/1.00/1

Table 21c.

Forcipomyia (*Schizoforcipomyia* *lerouxi* n. sp. - Measurements of key characters for single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		130	1.95 mm.
HEAD	Prob/Hd		56/90	0.62
	AR		119/112	1.06
	PR		23/7.5	3.07
THORAX	Legs	Fore TR	42/34	1.24
		Mid TR	34/56	0.61
		Hind TR	38/51	0.75
		Tib. spines	8	8
	Wing	L	70	1.05 mm.
		W	21	0.32 mm.
		CR	30/70	0.43
		vLR	98/86/143	1.14/1/1.66
		rs/r_1	35/21	1.67
		RR	12/10	1.20
		m_{3+4}/Cu_1	105/40	2.63
ABDOMEN (GENITALIA)	L/W	9th stern.	24/42	0.57
		9th trg.	20/42	0.48
		Bmr	31/18.5	1.68
		Tmr	22.5/5	4.50
		Aed	25/26	0.96
	Clsp	(b/c/b)	13/10/13	1.30/1/1.30

Table 21d.

Forcipomyia (*Schizoforcipomyia*) *lerouxi* n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		102	1.53 mm.
HEAD	Prob/Hd		60/80	0.75
	AR		95/95	1.00
	PR		23/11	2.09
THORAX	Legs	Fore TR	41/28	1.46
		Mid TR	37/46	0.80
		Hind TR	42/44	0.96
		Tib. spines	9	9
	Wing	L	55	0.83 mm.
		W	23	0.35 mm.
		CR	35/55	0.64
		vLR	69/58/102	1.19/1/1.76
		rs/r_1	44/26	1.69
		RR	20/14	1.43
		m_{3+4}/Cu_1	86/46	1.87
ABDOMEN	Smaller spmth	L	15	51.75μ
		W	10	34.50μ
	Larger spmth	L	16	55.20μ
		W	11	37.95μ

Table 22a.

Lasiohelea (*Thyridomyia*) *vertexcava* n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length (L)		106	1.59 mm.
	Width(W)/Depth(D)		28/22	1.27
HEAD	Lateral View	HR (L/D)	87.5/61	1.44
		OH/v	47/30	1.57
		qt/ts/sq	25/24/16	1.56/1.50/1
	Ventral View	L/W	53/57	0.93
		tt/ant	19/39	0.49
		qq/eyes	20/42	0.48
		qq/ss	20/51	0.39
		q (Fil/Tub)	50/5	10.00
		s (Fil/Tub)	25/3.5	7.14
		Eye (Ht/W)	5.5/10	0.55
THORAX	Ant. pseud.	L/W/D	37.5/48.5/28	1.33/1.73/1
	Proth. setae	*a* (Fil/Tub)	13/8	1.63
		b (Fil/Tub)	10/1.5	6.67

Table 22b.

Lasiohelea (Thyridomyia) vertexcava n. sp. - Measurements of key characters for single female pupa.

CHARACTER			ORIGINAL	CALCULATED
WHOLE PUPA	L		118	1.40 mm.
	W		36.5	0.43 mm.
	Cph/Abd		52/85	0.61
CEPHALO-THORAX	L/W		52/36.5	1.42
	Hd/th	Dorsal a.	8.5/37.5	0.23
		Ventral a.	19/39	0.48
	Resp. Horn	L/W	52/24	2.17
		TrL/W	37.5/3.7	10.29
		TrL/HL	37.5/52	0.72
		No. sp. pap. (upper & lower palisades)	17+22	39
ABDOMEN	3rd segt (L/W/D)		10/31/24	1/3.10/2.40
	Last segt (L/W/D)		56/46/45	1.24/1.02/1
	Term. proc. (L/W/D)		46/20/20	2.30/1.00/1

Table 22 c

Lasiohelea (**Thyridomyia**) **vertexcava** n.sp. - Measurements of key characters for three adult males

	CHARACTER		1	2	3	$\bar{x}$
WHOLE INSECT	Body length (L)		74	68	--	1.07 mm.
HEAD	Prob/Hd		--	--	37/61	0.61
	AR		65/77	55/67	74/87	0.84
	PR		15/5	15/5	17/5	3.13
THORAX	Legs	Fore TR	34/13	35/12	37/11	2.97
		Mid TR	32/14	33/14	34/16	2.26
		Hind TR	40/14	42/15	42/16	2.76
		Tib. spines	6	7	7	6.67
	Wing	L	44	43	44	0.66 mm.
		W	17	17	17	0.26 mm.
		CR	19.5/44	20/43	--	0.45
		vLR	51/40/95	48/41/95	--	1.22/1/2.35
		rs/r_1	35/20	40/20	--	1.88
		RR	14/14	13/14	--	0.97
		m_{3+4}/Cu_1	60/24	60/24	--	2.50
ABDOMEN (GENITALIA)	L/W	9th stern.	19/25	--	20/26	0.77
		9th trg.	13/25	--	14/26	0.53
		Bmr	23/10	--	23/10	2.30
		Tmr	20.5/4	--	21/4	5.19
		Aed	11/11	--	12/12	1.00
	clsp (b/c/b)		--	--	7/12.5/7	0.56/1/0.56

Table 22d.

Lasiohelea (*Thyridomyia*) *vertexcava* n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		60	0.90 mm.
HEAD	Prob/Hd		30/49	0.612
	AR		34/43.5	0.78
	PR		13/7	1.86
THORAX	Legs	Fore TR	29/10	2.90
		Mid TR	30/12	2.50
		Hind TR	35/11	3.18
		Tib. spines	6	6
	Wing	L	35	0.53 mm.
		W	19	0.29 mm.
		CR	18.5/35	0.53
		vLR	33/27/70	1.22/1/2.59
		rs/r_1	45/20	2.25
		RR	22/11	2.00
		m_{3+4}/Cu_1	58/28	2.07
ABDOMEN	Spmth	L	10	34.50µ
		W	9	31.05µ

TABLE 23a

Lasiohelea (*Thyridomyia*) *rugosa* n.sp. - Measurements of key characters for 10 full-grown third instar larvae

CHARACTER		SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
		1	2	3	4	5	6	7	8	9	10			
WHOLE	Body length(L)	84	85	85	87	81	79	85	84	85	86	1.26mm.	0.04mm.	0.01mm.
LARVA	Width (W)	9	9	10	10	9	9	9	9	9	9	0.14mm.	0.01mm.	0.002mm.
HEAD	Lat- HR(L/D)	42/31	42/30	42/30	44/30	38/28	41/29	41/29	42.5/32	42/30	42/30	1.39	0.04	0.01
	eral OH/v	25/14	25/14	25/14	25/14	22/13	25/14	23/12.5	25/14	24/14	24.5/14	1.77	0.05	0.02
	View qt/ts/sq	15/18/7.5	15/17.5/7.5	15/18/7.5	15/18/8	14/17/7.5	15/17.5/7	15/17.5/7.5	15/18.5/8	14/17.5/7	14/17/7.5	1.96/2.36/1	0.08/0.10/1	0.03/0.03/0.32
	L/W	31/29	30/29	31/30	29/28	27/27	29/27	28/27	30/28	28/27	29/28	1.04	0.01	0.003
	tt/ant	8/18	8/18	8/18	8/18	8/17	8/17	7.5/17	8/17.5	7.5/17	7.5/17	0.45	0.01	0.003
	Ven- qq/eyes	10/18.5	10/18.5	11/21	11/20	10.5/21	10/18.5	10/19	10/19	10.5/20	11/20	0.53	0.03	0.008
	tral qq/ss	10/23	10/23	11/25	11/23	10.5/22.5	10/22	10/22	10/23	10.5/23	11/23	0.45	0.02	0.01
	View q(Fil/Tub)	17/2	17/2	19/2	17/2	17/2	17/2	16.5/2	19/2	17/2	17.5/2	8.70	0.44	0.14
	s(Fil/Tub)	10/1	12/1.2	12/1.2	11/1.2	11/1.2	11/1.2	10.5/1.2	11/1.2	11/1.2	12/1.2	9.46	0.49	0.16
	Ēye	2.5/6	2.5/6	2.5/5.5	2/6	2/5	2.5/6	2/5	2.5/6	2/5.5	2/5.5	0.40	0.04	0.01
THORAX	Ant. pseud. L/W/D	18/20/13	19/20/14	18/20/14	19/21/14	18/20/14	18/19/14	17/19/13	18/20/13	18/19/13	18/20/13	1.33/1.46/1	0.05/0.07/1	0.02/0.02/0.32
	Proth. a(Fil/Tub)	15/6	15/6	15/6.5	15/7	14/5.5	15/6	14/5	15/5	15/5	15/5.5	2.60	0.28	0.09
	setae b̄(Fil/Tub)	10/3.5	10/3.5	10/4	10/3.5	10/4	10/4	10/3.5	10/3	10/3.5	10/4	2.76	0.27	0.08

TABLE 23b

Lasiohelea (*Thyridomyia*) *rugosa* n.sp. - Measurements of key characters for 10 male pupae

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE PUPA		L	126	123	117	122	113	105	123	120	112	112	1.76mm.	0.10mm.	0.03mm.
		W	30	30	28	29	29	27.5	30	29	29	28	0.43mm.	0.04mm.	0.01mm.
		Cph/Abd.	56/87	55/89	53/82	56/84	54/80	51/72	56/85.5	55/81	55/77	54/77	0.67	0.02	0.01
CEPHALOTHORAX	L/W		56/30	55/30	53/28	56/29	54/29	51/27.5	56/30	55/29	55/29	54/28	1.88	0.03	0.01
	Hd/Th.	Dorsal a.	9/33	9/32	9/31	10/31	9/31	9/30	10/33	10/30	10/30.5	9/30	0.30	0.02	0.01
		Ventral a.	20/49	21/49	20/46	20.5/46	20.5/46	21/47	21.5/49	21.5/49	21.5/45	20/44	0.45	0.02	0.01
	Resp. Horn	L/W	17/8	17/9	17/9	17/10	16/9	17/9.5	17/10	16/8.5	16.5/9.7	16/9	1.82	0.13	0.04
		TrL/W	11/2	10/2	11/2	11/2	10.5/2	11/2	10/2	10/2	11/2	11/2	5.33	0.24	0.08
		TrL/HL	11/17	10/17	11/17	11/17	10.5/16	11/17	10/17	10/16	11/16.5	11/16	0.64	0.03	0.01
		No.sp.pap.	7	7	6	8	6	5	5	4	6	5	5.90	1.20	0.38
ABDOMEN		3rd seg.(L/W/D)	12/20/20	11.5/20/20	10/20/18.5	10/20/19.5	11/20/20	10/19.5/18.5	10/20/20	10/20/20	10/20/20	10.5/19/19	1/1.90/1.87	1/0.13/0.12	0.32/0.04/0.04
		Sex.proc.(L/W.D)	22/15/15	23/14/12	20/14/11.5	23/13/12	21/13/12	20/13/12	23/13/12	21/13/12	22/12/11.5	21/13/11	1.80/1.10/1	0.15/0.08/1	0.05/0.02/0.32
		Term.proc.(L/W)	15/12	17/12	13/11	14.5/12	17/13	15/12	16/11	15/11	15/11	17/12	1.32	0.10	0.03

TABLE 23c

Lasiohelea (*Thyridomyia*) *rugosa* n.sp. - Measurements of key characters for 10 female pupae

CHARACTER		SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
		1	2	3	4	5	6	7	8	9	10			
WHOLE PUPA	L	112	113	123	110	129	105	115.5	115	109	100.5	1.70mm.	0.12mm.	0.04mm.
	W	27	28	30	28	32	26	29	27	28	26.5	0.42mm.	0.03mm.	0.01mm.
	Cph/Abd.	46.5/83	49/83	52/95	50/80	54/99	46/79	48/83	45/80	48/80	46/70	0.59	0.03	0.01
CEPH-ALO-THORAX	L/W	46.5/27	49/28	52/30	50/28	54/32	46/26	28/29	45/27	48/28	46/26.5	1.66	0.22	0.07
	Hd/Th. Dorsal a.	8/30	8/30.5	9/33	7.5/30	9/34	7/27	7/32	7/29	7.5/28	7/30	0.25	0.01	0.004
	Hd/Th. Ventral a.	18/41	18/44.5	18/44	18/45	20/47	17.5/40.5	17/45	17/40	18/43	18/41	0.42	0.02	0.01
	Resp. Horn L/W	15/8	16/10	16/9	16.5/9	16.5/8	16/10	15/8	15/9	15/8	16/10	1.78	0.15	0.05
	Resp. Horn TrL/W	10/1.5	10/2	10.5/2	11/2	11/2	11/2	10/2	10/2	10/1.5	11/2	5.56	0.63	0.20
	Resp. Horn TrL/HL	10/15	10/16	10.5/16	11/16.5	11/16.5	11/16	10/15	10/15	10/15	11/16	0.67	0.01	0.004
	Resp. Horn No.sp.pap.	5	6	5	5	5	6	6	5	5	6	5.40	0.52	0.16
ABDO-MEN	3rd seg.(L/W/D)	10.5/24/20	11/21.5/21	12/20/20.5	11/20/20	12/22/22	11/19/18	11.5/20/21	10.5/20/20	10/20/21	9/20/20	1/1.92/1.89	1/0.21/0.17	06 0.32/0.07/0.
	Last seg.(L/W/D)	39/29/30	36/32/31	39/30/30	38/30/29	40/30/31	37/29/28	38/30/30	35/28/30	37/29/28	35/30/30	1.26/1.00/1	0.08/0.02/1	0.32 0.02/0.01/
	Term.proc.(L/W)	17/12	18/13	16/11	16/12	17/12	14/12	17/12	15/11	16/11.5	16/12	1.37	0.08	0.02

TABLE 23d

Lasiohelea (*Thyridomyia*) *rugosa* n.sp. - Measurements of key characters for 10 adult males

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE INSECT	Body length(L)		107	100	88	95	91	103	92	90	89	92	1.42mm.	0.10mm.	0.03mm.
HEAD	Prob/Hd.		60/65	54/60	53/62	52/64	55/71	55/64	53/68	55/66	49/59	50/60	0.84	0.05	0.02
	AR		83/90	78/84	79/84	79/84	85/81	92/97	81/84	85/90	71/76.5	84/79	0.96	0.05	0.02
	PR		20/5.5	19/5	19/6	19/5.5	19/5	18.5/5	18/4.5	20/6	16/4.5	19/4.5	3.67	0.31	0.10
THORAX	LEGS	Fore TR	44/16	49/18	44/16	45.5/16.5	45/16	45/16	46/16	46/16	40/14	47/16	2.82	0.07	0.02
		Mid TR	38/17.5	46/19	46/19	44/20	43.5/19	45/19	42/18.5	45/20	40/16	46.5/20	2.32	0.10	0.03
		Hind TR	62/23	55/22	54/19	58/20	58/20	60/21	60/20	61/20	49.5/18	60/20	2.85	0.16	0.05
		Tib.spines	7	8	6	7	8	7	8	7	7	6	7.10	0.74	0.23
	WING	L	59	56	56	57	55.5	57	55	58	48	57	0.84mm.	0.14mm.	0.05mm.
		W	19	20	19	20	19	19.5	19	19.5	17	19	0.29mm.	0.04mm.	0.01mm.
		CR	27/59	26/56	26.5/56	28/57	27/55.5	27/57	26.5/35	27/58	23/48	26.5/57	0.47	0.01	0.003
		VLR	70/59/123	62/51/120	69/58/118	70/55/121	65/52/116	67/54/125	62/52/120	68/35/125	59/48/103	69/55/120	1.23/1/2.21	0.01/1/0.10	0.003/0.32/0.03
		rs/r_1	50/25	53/30	51/26	54/30	54/30	55/30	54/30	55/30	45/23	51.28	1.86	0.09	0.03
		RR	19/20	18/20	19/22	18/22	20/22	18/21	19/22	20/22	16/19	20/20	0.89	0.06	0.02
		m_{3+4}/cu_1	70/36	71/31	81/37	78/33	75/34	73/32	70/30	75/33	62/25	79/33	2.28	0.15	0.05
ABDOMEN (GENITALIA)	L/W	9th stern.	27/33	29.32	27/33	28/32	27/30	30.34	25/31	28/33	23/28.5	25/32.5	0.84	0.03	0.01
		9th terg.	14/33	14/32	15/33	15.5/32	15/30	16/34	16/31	16/33	13/28.5	16/32.5	0.47	0.03	0.01
		Bmr	24/11.5	25/12	22.5/11	22/10.5	23.5/11	25/11	24/11	25/11	21/9.8	24/11	2.15	0.08	0.02
		Tmr	25/4	25/4	23/4	24/4	24/4	24.5/4.5	23/4	25/4	20/3	24/4	6.04	0.34	0.11
		Aed.	16/20	17/19	17/20	17/20	16/19	17/20	16/19	17/19	15/17	17/20	0.86	0.01	0.002
	Clsp (b/c/b)		15/15/15	15/15/15	15/16/15	15/14/15	15/15/15	16/16/16	15/12.5/15	15/13/15	13/13/13	13/14/13	1.03/1/1.03	0.09/1/0.09	0.03/0.32/0.03

TABLE 23e

Lasichelea (Thyridomyia) rugosa n.sp. - Measurements of key characters for 10 adult females

CHARACTER		SPECIMEN NO. 1	2	3	4	5	6	7	8	9	10	$\bar{x}$	σ	$S_{\bar{x}}$
WHOLE INSECT	Body length (L)	91	93	89	83	72	73	79	86	79	76	1.23mm.	0.11mm.	0.04mm.
HEAD	Prob/Hd.	62/65	59/65	53/59	50/59	51/60	51/54	57/68	58/70	57/64	51/56	0.89	0.05	0.02
	AR	60/49	51/47	48.5/48	54/50	50/47	48/46.5	62/54	62/55	59/51	50/47	1.10	0.07	0.02
	PR	16/6.5	16/6	15/5.8	16/6.5	15/5.2	15/6	17/8	18/7	15/6.5	16/5	2.58	0.29	0.09
THORAX	LEGS Fore TR	39/15	37/14	37/13.5	37.5/14.5	36.5/13.5	36.5/14	40/16	43/17	41/15.5	34.5/13.5	2.61	0.08	0.03
	Mid TR	39.5/17	35/15.5	36/15	37/16	36/15	37/15	42/18	45/19	41/16	37/15	2.39	0.08	0.03
	Hind TR	49/20.5	47/18	48.5/17	47/17.5	45/17.5	45/17	51/21	54/22	50/19	47/18	2.59	0.15	0.05
	Tib.spines	7	8	7	7	7	7	7	7	7	7	7.10	0.32	0.10
	WING L	48	45	44	45	43	45	50.5	50	49	47	0.70mm.	0.12mm.	0.05mm.
	W	22.5	22	21	21.5	21	21.5	24.5	24.5	23	22	0.34mm.	0.06mm.	0.02mm.
	CR	24/48	24/45	23/44	23/45	22.2/43	24/45	26/50.5	26.5/50	25/49	25/47	0.52	0.02	0.01
	vLR	49/39/95	44/35/87	49/34/86	44/35.5/85	43/35/86	44/34/83	50/39/105	53/43/108	49/38/102	50/39/94	1.28/1/2.50	0.07/1/0.11	0.02/0.32/0.03
	rs/r_1	60/29	58/28	55/27	58/27	56/25	59/30	69/40	70/40	62/39	63/35	1.94	0.21	0.07
	RR	30/22	26/21	25/15	25/16	25/15	26/20	28/24	29/24	27/24	26/23	1.34	0.21	0.07
	m_{3+4}/cu_1	70/36	69/35	72/37	71/39	66/35	67/35	73/40	75/38	67/36	67/35	1.91	0.03	0.01
ABDOMEN	Spmth. L	14	14	14	15	14.5	15	16	15	12	15	49.85 μ	11.63 μ	0.23 μ
	W	13	13	13	13.5	13	13	14	13	10	12.5	44.16 μ	11.56 μ	3.66 μ
	Duct L	3.5	4	3	4	4	3.5	4	3.5	3	3	12.25 μ	0.48 μ	0.15 μ

[redacted]

Table 24a.

Lasiohelea (Thyridomyia) monilicornis (Goetghebuer) - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length (L)		150	2.25 mm.
	Width(W)/Depth(D)		24/22	1.09
HEAD	Lateral View	HR (L/D)	61/48	1.27
		OH/v	35/23	1.52
		qt/ts/sq	22/22/13	1.69/1.69/1
	Ventral View	L/W	45/45	1.00
		tt/ant	8/29	0.28
		qq/eyes	17/32	0.53
		qq/ss	17/40	0.43
		AR	4/9	0.44
		q (Fil/Tub)	32/5	6.40
		s (Fil/Tub)	18/25	7.2
		Eye (Ht/W)	3/9	0.33
THORAX	Ant. pseud.	L/W/D	30/25/17	1.77/1.47/1
	Proth. setae	a (Fil/Tub)	60/50	1.20
		b (Fil/Tub)	32/6	5.33

Table 24b.

Lasiohelea (*Thyridomyia*) *monilicornis* - Measurements of key characters for single male and female pupa.

CHARACTER			Female		Male	
			Original	Calculated	Original	Calculated
WHOLE PUPA	L		90	1.49 mm.	100	1.50 mm.
	W		28	0.42 mm.	30	0.45 mm.
	Cph/Abd		49/70	0.70	51/65	0.79
CEPHALO-THORAX	L/W		49/28	1.75	51/30	1.70
	Hd/th	Dorsal a	7/30	0.23	8/31.5	0.25
		Ventral a	19/41	0.46	22/45	0.49
	Resp. Horn	L/W	26/16	1.63	34/15	2.27
		TrL/W	20/3	6.67	29/3	9.67
		TrL/HL	20/26	0.77	29/34	0.85
		No. sp. pap. (upper & lower palisades)	18+13	18+13	18+15	18+15
ABDOMEN	3rd segt (L/W/D)		8/25/20.5	1/3.13/2.56	10/25/20.5	1/2.50/2.05
	Last segt (L/W/D)		40/29/29	1.38/1.00/1	43/42/34	1.27/1.24/1
	Term. proc. (L/W/D)		24/17.5/13	1.85/1.35/1	23/16/12	1.92/1.33/1
	Sex. proc. (L/W/D)		—	—	20/15/11	1.82/1.36/1

Table 24c.

Lasiohelea (Thyridomyia) monilicornis (Goetghebuer) - Measurements of key characters for two adult males.

CHARACTER			1	2	$\bar{x}$
WHOLE INSECT	Body length (L)		105	100	1.54 mm.
HEAD	Prob/Hd		47/80	42/61	0.64
	AR		92.5/96	89/84	0.96
	PR		—	20/5	4.00
THORAX	Legs	Fore TR	59/24	43/16	2.57
		Mid TR	53/22.5	46/19	2.39
		Hind TR	62/24	54/22.5	2.49
		Tib. spines	7	7	7
	Wing	L	67.5	58	0.94 mm.
		W	24	18.5	0.32 mm.
		CR	32/67.5	26/58	0.46
		vLR	84/68/150	67/49/142	1.30/1/2.55
		rs/r_1	61/45	45/30	1.43
		RR	12/30	12/28	0.42
		m_{3+4}/Cu_1	82/44	76/29	1.90
ABDOMEN (GENITALIA)	L/W	9th stern.	32/34	29/28	0.99
		9th trg.	13/34	16/28	0.48
		Bmr	31/12	26/10	2.59
		Tmr	25.5/5	25/4	5.68
		Aed	12/18	13/16	0.74
	Clsp	(b/c/b)	10/19/10	9/14.5/9	0.57/1/0.57

Table 24d.

Lasiohelea (*Thyridomyia*) *monilicornis* (Goetghebuer) - Measurements of key characters for two adult females.

CHARACTER			1	2	$\bar{x}$
WHOLE INSECT	Body length (L)		98	—	1.47 mm.
HEAD	Prob/Hd		38/57	—	0.67
	AR		47/54	—	0.87
	PR		19/6	—	3.17
THORAX	Legs	Fore TR	44/17	—	2.35
		Mid TR	47/19	—	2.47
		Hind TR	55/21	57/22	2.61
		Tib. spines	8	—	8
	Wing	L	57	61	0.89 mm.
		W	27	27	0.41 mm.
		CR	28.5/57	31/61	0.50
		vLR	60/43/115	64/45/120	1.41/1/2.67
		rs/r_1	69/41	74/45	1.66
		RR	26/30	25/32	0.82
		m_{3+4}/Cu_1	90/47	90/51	1.84
ABDOMEN (spmth)	L		23	—	79.35μ
	W		20	—	69.00μ
	Duct L		5	—	17.25μ

Table 25a.

Lasiohelea (*Thyridomyia*) *gossympina* n. sp. - Measurements of key characters for single male and female pupa.

CHARACTER			Female		Male	
			Original	Calculated	Original	Calculated
WHOLE PUPA	L		103	1.55 mm.	101	1.52 mm.
	W		25.5	0.38 mm.	25.5	0.38 mm.
	Cph/Abd		44/74	0.60	47.5/68.5	0.69
CEPHALO-THORAX	L/W		44/25.5	1.73	47.5/25.5	1.86
	Hd/Th	Dorsal a.	5/28.5	0.18	8/29.5	0.24
		Ventral a.	17.5/40	0.44	20/40	0.50
	Resp. Horn	L/W	28/13	2.15	28.5/13.5	2.11
		TrL/W	22/3	7.33	24/2.5	9.60
		TrL/HL	22/28	0.79	24/28.5	0.84
		No. sp. pap. (upper & lower palisades)	11+14	11+14	10+16	10+16
ABDOMEN	3rd segt (L/W/D)		10/19.5/19	1/1.95/1.90	9.5/19/19	1/2.00/2.00
	Last segt (L/W/D)		38/27/31	1.41/1/1.15	36/30/31	1.20/1/1.03
	Term. proc. (L/W/D)		25/13/12	2.08/1.08/1	26/14/11	2.36/1.27/1
	Sex. proc. (L/W/D)		---	---	18/10.5/9	2.00/1.17/1

Table 25b.

Lasiohelea (*Thyridomyia*) *gossympina* n. sp. - Measurements of key characters for three adult males.

CHARACTER			1	2	3	$\bar{x}$
WHOLE INSECT	Body length (L)		70.5	68	77	1.08 mm.
HEAD	Prob/Hd		40/56	38/62	44/62	0.68
	AR		66/75	62/72	66/73	0.91
	PR		17/5	17/5	17/5	3.40
THORAX	Legs	Fore TR	36/12.5	37/13	40/14	2.86
		Mid TR	35.5/15	37/16	40/16	2.39
		Hind TR	40/15	44/16	44/16	2.47
		Tib. spines	6	7	7	6.70
	Wing	L	46	46	49	0.71 mm.
		W	17	17.5	17	0.26 mm.
		CR	21.5/46	22/46	24/49	0.48
		vLR	53/45/96	51/45/99	58/51/108	1.15/1/2.15
		rs/r_1	42/23	46/25	48/26	1.84
		RR	18/17	16/18	19/18	1.00
		m_{3+4}/Cu_1	65/34	60/29	65/29	2.07
ABDOMEN (GENITALIA)	L/W	9th stern.	20/26	20/29.5	25/30	0.76
		9th trg.	14/26	18.5/29.5	16/30	0.57
		Bmr	21/9.5	21.5/10	23/10	2.22
		Tmr	18/4.5	16/4.5	18/4	4.02
		Aed	11/17.5	10.1/19	11/17	0.60
	Clsp (b/c/b)		7/14/7	6/15/6	7/16/7	0.45/1/0.45

Table 25c.

Lasiohelea (*Thyridomyia*) *gossympina* n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		60	0.90 mm.
HEAD	Prob/Hd		37/51	0.73
	AR		46/44	1.05
	PR		14/6	2.33
THORAX	Legs	Fore TR	34/12	2.83
		Mid TR	34/13	2.62
		Hind TR	41/15	2.73
		Tib. spines	7	7
	Wing	L	40	0.60 mm.
		W	21	0.32 mm.
		CR	21.5/40	0.54
		vLR	37/31/80	1.19/1/2.58
		rs/r_1	60/30	2.00
		RR	26/19	1.37
		m_{3+4}/Cu_1	59/30	1.97
ABDOMEN (spmth)	L		12	41.40μ
	W		11	37.95μ
	Duct L		3	10.35μ

Table 26a.

Lasiohelea (*Lasiohelea*) *propria* n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length (L) Width(W)/Depth(D)		192 21/20	2.88 mm. 1.05
HEAD	Lateral View	HR (L/D) OH/v qt/ts/sq	74/50 43/21 27/28/15	1.48 2.05 1.80/1.87/1
	Ventral View	L/W tt/ant qq/eyes qq/ss AR *q* (Fil/Tub) *s* (Fil/Tub) Eye (Ht/W)	51/52 16/34 16/41 16/48 18.5/3 30/4 21/3 5/8	0.98 0.47 0.39 0.33 2.75 7.50 7.00 0.63
THORAX	Ant. pseud.	L/W/D	28/31/20	1.40/1.55/1
	Proth. setae	*a* (Fil/Tub) *b* (Fil/Tub)	24/17 16/9	1.41 1.78

Table 26b.

Lasiohelea (*Lasiohelea*) *propria* n. sp. - Measurements of key characters for two male pupae.

CHARACTER			1	2	$\bar{x}$
WHOLE PUPA	L		138	135	2.04 mm.
	W		34	31	0.36 mm.
	Cph/Abd		59/93	61/95	0.64
CEPHALO-THORAX	L/W		59/34	61/31	1.85
	Hd/th	Dorsal a.	8/36	8/33	0.23
		Ventral a.	21/53	21/53.5	0.40
	Resp. Horn	L/W	35/8	31/7.5	4.25
		TrL/W	28/3	24/2.5	9.28
		TrL/HL	28/35	24/31	0.79
		No. sp. pap.	8	7	7.50
ABDOMEN	3rd segt (L/W/D)		13.5/20/17	13.5/19.5/18	1/1.46/1.30
	Term. proc. (L/W/D)		27/20/13	29/19/13	2.15/1.50/1
	Sex. proc. (L/W/D)		27/15/15	27/15/15	1.80/1.00/1

Table 26c.

Lasiohelea (*Lasiohelea*) *propria* n. sp. - Measurements of key characters for two adult males.

CHARACTER			1	2	$\bar{x}$
WHOLE INSECT	Body length (L)		100	96	1.47 mm.
HEAD	Prob/Hd		42/72	40/68	0.59
	AR		90/96	92/94	0.96
	PR		13/6.5	13.5/7	1.97
THORAX	Legs	Fore TR	50/23	51/23	2.20
		Mid TR	47/26	47/26	1.81
		Hind TR	60/32	60/32	1.88
		Tib. spines	7	8	7.50
	Wing	L	59	60	0.90 mm.
		W	20.5	20.5	0.31 mm.
		CR	33.5/59	33/60	0.56
		vLR	78/66/125	78/66/124	1.18/1/1.89
		rs/r_1	67/30	70/30	2.28
		RR	37/20	37/20	1.85
		m_{3+4}/Cu_1	85/36	84/35	2.38
ABDOMEN (GENITALIA)	L/W	9th stern.	25/40	24/41	0.61
		9th trg.	11/40	11/41	0.27
		Bmr	31/13	32/14	2.84
		Tmr	28/4	27/4	6.88
		Aed	17/29	16/30	0.56
	Clsp	(b/c/b)	13/9.5/13	12/10/12	1.28/1/1.28

Table 26d.

<u>Lasiohelea</u> (<u>Lasiohelea</u>) <u>propria</u> n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		80	1.20 mm.
HEAD	Prob/Hd		40/75	0.53
	AR		88/52	1.69
	PR		14/8.5	1.65
THORAX	Legs	Fore TR	50/20	2.50
		Mid TR	44.5/23	1.94
		Hind TR	63/30	2.10
		Tib. spines	7	7
	Wing	L	54.5	0.82 mm.
		W	25	0.38 mm.
		CR	34/54.5	0.62
		vLR	59/50/106	1.18/1/2.12
		rs/r_1	95/30	3.17
		RR	50/28	1.79
		m_{3+4}/Cu_1	85/44	1.93
ABDOMEN	Spmth	L	20	69.00μ
		W	15.5	53.48μ

Table 27a.

Lasiohelea (Lasiohelea) uncuspromissa n. sp. - Measurements of key characters for single fourth-instar larva.

CHARACTER			ORIGINAL	CALCULATED
WHOLE LARVA	Body length (L) Width(W)/Depth(D)		178.5 20/19.5	2.68 mm. 1.03
HEAD	Lateral View	HR (L/D) OH/v qt/ts/sq	10.6/8 61/40 36/35/25	1.33 1.53 1.44/1.40/1
	Ventral View	L/W tt/ant qq/eyes qq/ss AR q (Fil/Tub) s (Fil/Tub) Eye (Ht/W)	76/75 24/47 26/56 26/67 30/17 51/5 35/4 10/13.5	1.0 0.51 0.46 0.39 1.77 10.20 8.75 0.74
THORAX	Ant. pseud.	L/W/D	51/49/39	1.31/1.26/1
	Proth. setae	a (Fil/Tub) b (Fil/Tub)	33/27 30/18	1.22 1.67

Table 27b.

Lasiohelea (Lasiohelea) uncuspromissa n. sp. - Measurements of key characters of single female pupa.

CHARACTER			ORIGINAL	CALCULATED
WHOLE PUPA	L		122.5	1.84 mm.
	W		30	0.45 mm.
	Cph/Abd		80/115	0.70
CEPHALO-THORAX	L/W		74/42	1.76
	Hd/th	Dorsal a.	16/16	0.24
		Ventral a.	32/79	0.41
	Resp. Horn	L/W	35/12.5	2.80
		TrL/W	26/2.5	10.40
		TrL/HL	26/35	0.74
		No. sp. pap.	7	7
ABDOMEN	3rd segt (L/W/D)		15/30/25	1/2.00/1.67
	Last segt (L/W/D)		12/12/11.5	1.09/1.09/1
	Term. proc. (L/W/D)		41/22/22	1.86/1.00/1

Table 27c.

Lasiohelea (*Lasiohelea*) *uncuspromissa* n. sp. - Measurements of key characters of single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		8	1.45 mm.
HEAD	Prob/Hd		42/64	0.66
	AR		93/86	0.96
	PR		11.3/6	1.88
THORAX	Legs	Fore TR	50/22	2.27
		Mid TR	47/24.5	1.88
		Hind TR	61/30	2.03
		Tib. spines	8	8
	Wing	L	44	0.84 mm.
		W	14	0.26 mm.
		CR	26/44	0.59
		vLR	14/12/2.15	1.17/1/1.79
		rs/r_1	12/5	2.40
		RR	49.5/43	1.15
		m_{3+4}/Cu_1	70/27	2.59
ABDOMEN (GENITALIA)	L/W	9th stern.	25/30	0.83
		9th trg.	31/30	1.03
		Bmr	30/11	2.73
		Tmr	25/4	6.43
		Aed	22/37	0.60
	Clsp	(b/c/b)	11.5/7/11.5	1.64/1/1.64

Table 27d.

<u>Lasiohelea</u> (<u>Lasiohelea</u>) <u>uncuspromissa</u> n. sp. - Measurements of key characters of single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		87.3	1.31 mm.
HEAD	AR		116/65.5	1.77
	PR		12.5/8.3	1.50
THORAX	Legs	Fore TR	50/20	2.50
		Mid TR	49.5/22	2.25
		Hind TR	64/28	2.11
		Tib. spines	8	8
	Wing	L	51.5	0.77 mm.
		W	23.3	0.35 mm.
		CR	38/51.5	0.66
		vLR	66/59.5/101	1.11/1/1.70
		rs/r_1	90/40	2.25
		RR	78/59	1.31
		m_{3+4}/Cu_1	27/12	2.25
ABDOMEN	Spmth	L	18	62.07µ
		W	15	51.72µ

TABLE 28a

Neoforcipomyia saundersi n.sp. - Measurements of key characters for 10 full-grown fourth-instar larvae

	CHARACTER		SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE LARVA		Body length(L)	175	150	175	190	206	162	171	198	185	180	2.69mm.	0.25mm.	0.08mm.
		Width(W)/Depth(D)	21/21	21/20	24/23	23/25	26/27	19/19	23/22	25/25	22/22	26/25	1.01	0.05	0.02
HEAD	Lateral View	HR (L/D)	83/55	84/60	76/55	83/57	85/58	81/58	86/56	78/53	81/55	83/55	1.46	0.05	0.02
		OH/v	46/29	55/27	47/26	47/27	50/29	55/28	51/26	48/26	49/26	48/26	1.84	0.13	0.04
		qt/ts/sq	21/23/16	22/26/15	20/24/14	21/25/16	22/30/17	20/24/15	21/25/15	20/23/16	21/24/15	20/24/16	1.35/1.60/1	0.13/0.15/1	0.04/0.05/0.32
	Ventral View	L/W	56/63	61/62	60/63	59/62	58/65	55/58	58/62	53/54	60/64	60/62	0.94	0.04	0.01
		tt/ant	17/40	18/42	18/44	18/43	17/45	16/40	17/41	16/40	18/42	18/42	0.41	0.08	0.02
		qq/eyes	23/44	23/44	23/45	23/44	24/45	21/42	22/43	21/40	23/44	23/43	0.52	0.01	0.003
		qq/ss	23/57	23/57	23/59	23/58	24/59	21/51	22/55	21/50	23/58	23/55	0.41	0.01	0.003
		AR(L/W)	15/2	15/2	15/2	17/2.5	18/3	17/2	18/2	15/2	16/2	15/2.5	7.43	0.97	0.31
		q(Fil/Tub)	50/5	50/6	45/5	45/6	52/5	51/5	50/6	45/5	43/5	47/6	8.92	0.99	0.31
		s(Fil/Tub)	26/3	30/3.5	28/3	34/3	27.5/3	26.3	27/3.5	30/3	27/3	28/3	9.18	0.56	0.18
		Eye (Ht/W)	6/9	6/9	6/9	6/9	6/9	6/9	6/9	6/9	6/8.5	6/9	0.67	0.01	0.003
THORAX	Ant. pseud.	L/W/D	37/30/25	24/25/24	35/26/27	39/26/24	38/30/25	35/38/25	35/28/26	36/27/25	38/29/25	36/29/22	1.47/1.12/1	0.24/0.23/1	0.08/0.07/0.32
	Proth. setae	a(Fil/Tub)	35/54	40/45	43/43	42/44	46/47	40/47	46/46	38/38	40/44	43/43	1.10	0.17	0.05
		b(Fil/Tub)	30/43	32/43	32/32	32/43	33/46	32/45	35/46	29/36	33/42	35/43	1.30	0.12	0.04

TABLE 28b

Neoforcipomyia saundersi n.sp. - Measurements of key characters for 10 male pupae

CHARACTER		SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
		1	2	3	4	5	6	7	8	9	10			
WHOLE PUPA	L W Cph/Abd.	145 41 71/97	139 39 69/93	155 42 73/105	147 41 73/98	145 39 72/100	133 38 65/94	143 42 72/96	138 35 66/95	138 37 69/90	138 40 67/97	2.13mm. 0.59mm. 0.72	0.09mm. 0.03mm. 0.26	0.03mm. 0.01mm. 0.08
CEPHA-LO-THORAX	L/W	71/41	69/39	73/42	73/41	72/39	65/38	72/42	66/35	69/37	67/40	1.77	0.06	0.02
	Hd/Th. Dorsal a. Ventral a.	11/39 30/56	9/33 29/57	13/43 35/64	13/38 34/60	13/38 29/58	10/37 28/56	10/40 29/60	6/35 30/60	9/39 30/60	8/36 27/60	0.27 0.51	0.06 0.04	0.02 0.01
	L/W Resp. TrL/W Horn. TrL/HL No.sp.pap.	33/14 20/3 20/33 11	28/15.5 16/4 16.28 12	33/15 23/4 23/33 11	39/15 28/4 28/39 11	35/13 23/3 23/35 11	35/13 23/3.5 23/35 11	29/15 17/4 17/29 11	34/14 23/4 23/34 10	34/15 22/4 22/34 10	35/14 24/4 24/35 11	2.35 5.92 0.65 10.90	0.30 1.15 0.05 0.57	0.09 0.36 0.02 0.18
ABDO-MEN	3rd segt.(L/W/D) Sex proc.(L/W/D) Term.proc.(L/W)	13/25/25 55/16/16 24/16	12/23/22 51/14/14 23.5/16	14/29/27 54/15/19 20/15	13/27/25 53/17/14 21.5/15	13/27/22 53/15/14 24/16	13/27/23 53/15/14 24/17	12/29/25 53/15/14 22/15.5	12/24/22 50/14/14 26/16	12/26/22 49/13/15 23/16	12/27/25 47/14/14 26/17	1/2.10/1.89 3.51/1.00/1 2.81	1/0.15/0.13 0.29/0.12/1 0.42	0.32/0.05/0.04 0.09/0.04/0.32 0.13

TABLE 28c

Neoforcipomyia *saundersi* n.sp. - Measurements of key characters for 10 female pupae

CHARACTER		SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
		1	2	3	4	5	6	7	8	9	10			
WHOLE PUPA	L	136	120	138	125	123	135	125	133	128	133	1.94mm.	0.09mm.	0.03mm.
	W	38	34	39	35	37	38	34	38	36	36	0.55mm.	0.03mm.	0.01mm.
	Cph/Abd.	64/95	60/83	66/95	63/83	62/84	66/90	60/85	65/91	60/87	64/91	0.71	0.03	0.01
CEPH-ALO-THORAX	L/W	64/38	60/34	66/39	63/35	62/37	66/38	60/34	65/38	60/36	64/36	1.73	0.02	0.01
	Hd/Th. Dorsal a.	6/33	5/33	10/39	6/37	6/34	7/40	6/35	6/34	7/36	7/33	0.19	0.03	0.01
	Hd/Th. Ventral a.	25/56	26/56	30/56	30/59	25/55	29/57	27/54	30/59	27/52	27/57	0.49	0.03	0.01
	Resp. Horn L/W	32/14	31/12	35/16	31/15	30/14	39/15	37/13	31/16	31/14	35/14	2.34	0.29	0.09
	Resp. Horn TrL/W	18/4	19/4	21/4	14/4	19/3	25/3.5	25/3.5	14/4	20/3	23/3	5.65	1.73	0.55
	Resp. Horn TrL/HL	18/32	19/31	21/35	14/31	19/30	25/39	25/37	14/31	20/31	23/35	0.59	0.08	0.03
	Resp. Horn No.sp.pap.	12	9	12	11	10	11	9	10	8	11	10.30	1.34	0.42
ABDO-MEN	3rd segt.(L/W/D)	12/28/22	12/25/23	13/27/25	12/25.5/24	12/27/25	13/28/25	12/24/20	13/26/21	12/25/22.5	12/25/24	1/2.12/1.88	1/0.10/0.14	0.32/0.03/0.04
	Last segt.(L/W/D)	52/45/46	48/42/42	53/43/49	42/43/46	42/45/43	52/50/46	44/39/43	48/38/40	48/37/44	44/41/42	1.12/1/1.05	0.12/1/0.08	0.04/0.32/0.03
	Term. proc.(L/W)	24/13	26/15	24/14	27/15	24/12	25/14	24/15	23/13.5	24/13	23/13	2.68	0.38	0.12

TABLE 28d

Neoforcipomyia *saundersi* n.sp. - Measurements of key characters for 10 adult males

CHARACTER			SPECIMEN NO.										$\bar{X}$	σ	$S_{\bar{X}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE INSECT		Body length (L)	115	117	117	122	125	110	120	130	125	126	1.81mm.	0.09mm.	0.03mm
HEAD		Prob/Hd.	42/81	46/84	40/80	43/79	46/80	41/81	41/82	46/83	47/81	42/87	0.53	0.03	0.01
		AR	119/104	120/111	118/107	122/107	119/95	119/104	120/104	123/107	129/108	117/105	1.15	0.04	0.01
		PR	14/7	14/6.5	14/6	13/6.5	14/6.5	13.5/6	15/7	15/5	13/6	15/6.5	2.25	0.29	0.09
THORAX	LEGS	Fore TR	62/25	59/24	59/23	58/25	56/23	57/24	58/24	60/24	60/26	57/24	2.42	0.09	0.03
		Mid TR	60/25	61/27	57/22	58/25	59/25	52/24	57/26	61/25	60/27	58/25	2.33	0.13	0.04
		Hind TR	70/28	75/28	70/26	73/27	69/29	69/26	70/26	73/26	74/28	77/27	2.68	0.11	0.03
		Tib.spines	7	8	7	7	7	8	7	8	8	8	7.50	0.53	0.17
	WING	L	70	72.5	69	68	69	67	71	72	74	70	1.05mm.	0.01mm.	0.003m
		W	23	23.5	21	22	23	23	23	23	25	23.5	0.35mm.	0.02mm.	0.005m
		CR	35/70	35/72.5	34/69	35/68	35/69	35/67	38/71	37/72	36.5/74	36/70	0.51	0.01	0.004
		vLR	97/82/150	96/82/154	93/80/148	94/79/154	93/82/150	88/80/150	96/84/160	97/84/166	98/82/169	97/83/155	1.16/1/1.90	0.03/1/0.15	0.04/0.32
		rs/r_1	60/32	61/38	60/32	60/32	67/33	70/36	73/41	70/38	70/38	67/34	1.88	0.12	0.04
		RR	23/24	22/26	25/24	22/24	28/25	29/23	30/28	27/31	25/28	26/26	1.00	0.13	0.04
		m_{3+4}/cu_1	100/40	99/43	85/39	94/40	92/40	94/39	93/40	94/40	99/45	98/41	2.33	0.09	0.03
ABDOMEN (GENITALIA)	L/W	9th stern.	20/38	20/38	19/36	18/36	19/36	18/39	20/39	20/39	19/39	17/38	0.50	0.03	0.01
		9th terg.	20/38	24/38	22/36	22/36	22/36	22/39	21/39	26/39	22/39	22/38	0.59	0.05	0.02
		Bmr	31/12	31/13	30/11	29/11	30/12	28/12	30/11	31/11	33/12	32/12	2.61	0.15	0.05
		Tmr	29/4	28/4	29/4	30/4	26/4	29/3.5	29/4	29/4	31/4	30/4	7.35	0.46	0.15
		Aed.	18/17	19/19	20/18	19/20	17/18	18/19	20/20	18/20	21/20	22/18	1.02	0.10	0.03
		Clsp (b/c/b)	18/16/18	18/18/18	18/17/18	19/12/18	19/18/18	18/17/18	18/20/18	19/18/19	17/19/17	18/16/17	1.09/1/1.07	0.10/1/0.15	0.03/0.3

TABLE 28e

Neoforcipomyia saundersi n.sp. - Measurements of key characters for 10 adult females

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE INSECT		Body length(L)	119	106	100	102	105	100	94	108	100	109	1.56mm.	0.10mm.	0.03mm.
HEAD		Prob/Hd.	46/83	43/80	42/81	43/82	44/80	44/80	42/75	45/82	43/80	46/82	0.54	0.02	0.01
		AR	119/60	115/55	117/53	119/53	120/55	119/52	110/54	129/51	119/57	124/54	2.20	0.16	0.05
		PR	13/9	14/10	13/9	11.5/8.5	13.5/4.5	15/10	15/9	13/9.5	12.5/9	14/9	1.45	0.10	0.03
THORAX	LEGS	Fore TR	58/20	59/21	58/20	59/21	62/22	57/21	54/20	61/22	60/22	65/22	2.81	0.08	0.02
		Mid TR	56/20	55/20	54/21	56/20	57/22	57/21	50/19	59/22	58/22	62/23	2.69	0.09	0.03
		Hind TR	67/24	72/25	67/23	70/24	71/26	65/23	66/23	74/25	74/26	77/25	2.88	0.08	0.02
		Tib.spines	7	7	7	7	7	7	7	8	8	8	7.30	0.48	0.15
	WING	L	62	60	58	61	62	59	56	61	62.5	62.5	0.91mm.	0.01mm.	0.009mm.
		W	29	28	26	29	30	28	27	29	29	29	0.43mm.	0.02mm.	0.01mm.
		CR	33/62	34/60	32/58	34/61	36/62	33/59	31/56	35/61	35/62.5	35/62.5	0.56	0.01	0.003
		vLR	69/59/128	68/58/126	68/57/126	68/58/126	76/61/135	72/61/126	64/54/122	71/60/132	76/66/136	71/59/132	1.19/1/2.18	0.07/1/0.17	0.02/0.32/0.06
		rs/r_1	78/37	82/41	75/35	80/41	83/42	72/35	71/36	84/43	80/37	85/42	2.04	0.07	0.02
		RR	30/30	40/29	32/29	37/29	42/28	33/26	33/27	35/30	36/28	40/28	1.26	0.15	0.05
		m_{3+4}/cu_1	90/52	90/50	83/46	90/52	96/54	89/49	80/47	90/50	96/52	96/57	1.77	0.06	0.02
ABDOMEN	Smaller Spmth.	L	19	17	16	17	18	17	17	18	17	18	261 μ	13.41 μ	4.25 μ
		W	16	14	15	16	17	15	16	17	15	15	234 μ	14.49μ	4.59μ
		Duct L	4	3.5	3	4	4	4	5	3	5	4	59.25μ	10.29μ	3.26μ
	Larger Spmth.	L	20	19	18	18	20	18	18	18	18	18	277.5μ	12.75μ	4.04μ
		W	16	15	16	16	18	15	15	17	17	16	241.5μ	14.91μ	4.71μ
		Duct L	4	4	3	4	4	4	4	4	4	4	58.5μ	4.80μ	1.52μ

TABLE 29a

Neoforcipomyra eques (Johannsen) - Measurements of key characters for 10 full-grown fourth-instar larvae

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE LARVA		Body length (l)	170	162	185	182	175	177	150	154	189	190	2.60mm.	0.21mm.	0.07mm.
		Width(W)/Depth(D)	20/26	18/24	26/28	24/25	21/23	20/24	20/19	20/21	28/30	22/27	0.89	0.09	0.03
HEAD	Lat-eral View	HR(L/D)	70/50	70/50	69/50	69/50	70/50	69/50	69/49	69/48	71/52	70/50	1.40	0.03	0.01
		OH/V	46/20	41/21	38/18	40/21	44/22	44/22	43/20	43/20	48/22	43/22	2.07	0.09	0.03
		qt/ts/sq	16/25/14	19/26/14	19/25/13	15/24/12	15/23/12	16/22/12	16/22/12	15/22/12	16/24/13	16/23/12	1.57/1.43/1	0.16/0.15/1	0.05/0.05/0.32
	Ventral View	L/W	49/51	50/52	48/52	48/53	50/53	50/52	47/49	49/52	51/56	48/53	0.94	0.02	0.01
		H/ant	16/33	16/36	16/35	16/35	16/35	16/35	15/32	16/35	18/38	16/36	0.46	0.01	0.004
		qq/eyes	20/37	21/39	22/40	20/40	21/40	21/39	20/37	21/39	23/42	20/39	0.53	0.01	0.004
		qq/ss	20/43	21/44	22/45	20/43	21/45	21/44	20/41	21/45	23/50	20/45	0.47	0.01	0.003
		AR(L/W)	15/2	15/2	14/2	13/2	14/2	14/2	14/2	14/2	16/2.5	15/2	7.04	0.39	0.12
		(Fil/Tub)	43/6	42/6	44/6	43/6	46/6	48/6	45/6	41/6	43/6.5	44/6	7.26	0.21	0.07
		s(Fil/Tub)	22/4	26/4	25/4	26/4	26/4	27/4	22/4	25/4	25/4	22/4	6.15	0.47	0.15
		$\bar{E}$ye(H /W)	7/9	5/9	5/9	6/8.5	6/9	6/9	5/9	5/9	6/9	6/10	0.63	0.08	0.02
THORAX	Ant. pseud.	L/W/D	38/32/25	31/30/20	35/33/28	35/32/24	35/31/20	35/31/19	34/28/22	33/32/21	35/33/22	35/34/22	1.29/1.88/1	0.09/0.04/1	0.03/0.01/0.32
	Proth. setae	a(Fil/Tub)	21/25	20/26	25/27	19/23	20/26	22/27	21/26	21/26	19/26	21/25	1.23	0.08	0.03
		b(Fil/Tub)	18/21	18/22	24/25	18/19	18/23	18/24	18/22	18/22	19/23	19/23	1.20	0.10	0.03

TABLE 29b

Neoforcipomyia eques (Johannsen) - Measurements of key characters for 10 male pupae

CHARACTER		SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
		1	2	3	4	5	6	7	8	9	10			
WHOLE PUPA	L W Cph/Abd.	139 38 67/91	126 35 65/87	122 33 63/80	135 39 70/94	135 38 72/94	127 33 64/85	128 35 66/85	120 37 70/86	133 37 69/87	129 39 67/89	1.94mm. 0.55mm. 0.77	0.09mm. 0.03mm. 0.03	0.03mm. 0.01mm. 0.01
CEPHALO-THORAX	L/W	67/38	65/35	63/33	70/39	72/38	64/33	66/35	70/37	69/37	67/39	1.85	0.07	0.02
	Hd/Th. Dorsal a. Ventral a.	9/41 33/64	6/32 29/58	10/35 29/56	10/37 30/55	10/40 26/60	10/37 27/52	9/37 28/59	10.40 30/60	11/38 28/57	7/35 28/60	0.25 0.50	0.03 0.02	0.01 0.01
	Resp. Horn L/W TrL/W TrL/HL No.sp.pap.	23/12 17/2.5 17/23 8	20/11 15/2.5 15/20 8	17/12 10/2 10/17 6	19/13 14/2 14/19 6	17/13 12/2 12/17 6	20/13 15/3 15/20 7	22/13 17/3 17/22 7	20/13 16/2 16/20 7	21/13 15/2.5 15/21 7	19/13 14/2.5 14/19 8	1.58 6.11 0.73 7.00	0.19 0.93 0.06 0.26	0.06 0.29 0.02 0.08
ABDOMEN	3rd segt.(L/W/D) Sex.proc.(L/W/D) Term.proc.(L/W)	12/29/23 37/15/12 6/5	12/25/21 37/15/12 4/3	12/24/21 34/15/12 5/5	10/29/22 40/15/12 6/5	13/26/23 42/14.5/12 6/4	12/23/21 37/14/12 6/5	11/28/24 38/16/12 7/5	12/30/24 37/13/14 7/5	12/25/22 37/14/13 7/6	11/26/23 37/13/13 6/6	1/2.27/1.92 3.04/1.17/1 1.24	1/0.43/0.27 0.25/0.13/1 0.17	1/0.13/0.09 0.08/0.04/0.32 0.05

[redacted]

TABLE 29c

Neoforcipomyia eques (Johannsen) - Measurements of key characters for
10 female pupae

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE PUPA		L	116	123	133	120	111	119	108	111	117	117	1.76mm.	0.11mm.	0.03mm.
		W	33	36	35	32	35	35	33	37	36	33	0.52mm.	0.03mm.	0.01mm.
		Cph/Abd.	60/77	64/80	65/88	57/80	63/68	65/77	59/71	63/73	63/77	61/76	0.81	0.06	0.02
CEPHALO-THORAX	L/W		60/33	64/36	65/35	57/32	63/35	65/35	59/33	63/37	63/36	61/33	1.80	0.05	0.02
	Hd/Th.	Dorsal a.	6/32	7/38	10/40	7/32	9/37	6/35	6/33	7/35	7/35	7/36	0.20	0.03	0.01
		Ventral a.	22/54	28/59	26/58	27/52	22/52	26/59	22/53	22/52	23/54	23/54	0.44	0.04	0.01
	Resp. Horn	L/W	22/12	20.14	21/13	20/12	22/12	21/12	19/11	22/13	20/13	20/13	1.66	0.14	0.04
		TrL/W	17/3	15/2	15/2	13/3	16/2	15/2	14/1.5	16/2	14/2	15/215	7.08	1.42	0.45
		TrL/HL	17/22	15/20	15/21	13/20	16/22	15/21	14/19	16/22	14/20	15/20	0.72	0.04	0.01
		No.sp.pap.	7	8	8	8	7	7	7	7	7	7	7.30	0.48	0.15
ABDOMEN		3rd segt.(L/W/D)	12/23/20	11/27/22	13/25/24	11/26/20	9/24/24	12/25/21	10/23/22	10/26/26	10/28/25	12/25/21	1/2.32/2.08	1/0.30/0.38	0.32/0.10/0.12
		Last segt.(L/W/D)	45/30/34	43/35/37	41/38/37	45/37/35	43/32/38	43/34/34	44/38/34	45/43/32	44/39/37	43/37/32	1.21/1/1.00	0.13/1/0.13	0.04/0.32/0.04
		Term.proc.(L/W)	8/5	7/6	7/6	5/4	7/5	7/6	7/6	7/6	7/4	7/6	1.29	0.09	0.03

TABLE 29d

Neoforcipomyia eques (Johannsen) - Measurements of key characters for 10 adult males

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE INSECT		Body length(L)	112	115	105	115	115	107	118	109	110	110	1.67mm.	0.06mm.	0.01mm.
HEAD		Prob/Hd.	54/90	50/82	50/82	51/82	51/90	51/85	52/90	50/80	51/81	50/82	0.61	0.03	0.01
		AR	23/25	93/95	87/84	90/100	88/90	96/98	105/103	87/90	83/82	97/98	0.98	0.05	0.01
		PR	14/6.5	15/6	15/6	15/6.5	14/6	14/6	15/6.2	13/6	16/7	13.5/6	2.33	0.12	0.04
THORAX	LEGS	Fore TR	12.5/5.5	45/25	45/20	51/24	46/21	49/22	50/22	42/18	50/22	47/22	2.19	0.15	0.05
		Mid TR	11.5/6	47/27	45/23	51/25	45/23	47/24	50/25	44/22	50/24	49/25	1.96	0.10	0.03
		Hind TR	74/33	65/31	64/26	66/30	60/27	62/27.5	69/30	64/25	68/28	64/29	2.30	0.15	0.05
		Tib.spines	8	7	7	8	7	7	7	7	7	7	7.20	0.42	0.13
	WING	L	74	66	61.5	67	63.5	62.5	71	62	68	68	1.00mm.	0.02mm.	0.02mm.
		W	21	23	21	24	23	21	4	21	25	23	0.34mm.	0.02mm.	0.01mm.
		CR	36.5/74	31/66	28/61.5	31/67	32/63.5	31/62.5	33/71	30/62	33/68	33/68	0.48	0.02	0.01
		VLR	96/82/160	80/70/140	75/65/136	71/62/139	80/70/138	76/66/136	87/75/149	72/60/127	85/72/148	82/72/150	1.16/1/2.06	0.02/1/0.19	0.01/0.32/0.09
		rs/r_1	60/25	57/30	54/27	64/30	60/28	58/29	60/31	56/29	62/38	62/29	2.08	0.59	0.19
		RR	32/25	33/23	31/22	31/21	27/21	24/22	22/22	23/21	26/25	26/25	1.22	0.18	0.06
		m_{3+4}/cu_1	100/45	94/36	80/30	99/48	83/42	89/40	96/48	90/40	104/50	94/44	2.22	0.24	0.08
ABDOMEN (GENITALIA)		9th stern.	22/35	22/34	19/32	20/34	20/32	18/31	20/34	20/32	20/35	22/34	0.61	0.01	0.003
		9th terg.	22/35	22/34	17/32	22/34	22/32	25/31	23/34	20/32	25/35	25/34	0.67	0.02	0.01
	L/W	Bmr	33/12	28/11	26/9	32/11	27/10	32/10	32/11	26/9	31/10	31/10.5	2.88	0.20	0.06
		Tmr	29/5	26/5	23/4	29/5.5	25/4	25/5	28/5	24/4.5	25/5	23/4.5	5.43	0.40	0.13
		Aed.	18/18	18/18	17/13	18/18	18/17	22/16	24/18	17/17	18/18	18/17	1.11	0.16	0.05
		Clsp (b/c/b)	19/14/19	18/12/18	16/12/16	19/15/19	17/13/16	17/14/18	18/15/19	16/14/17	17/16/17	18/14/19	1.27/1/1.27	0.12/1/0.12	0.04/0.32/0.04

TABLE 29e

Neoforcipomyia eques (Johannsen) - Measurements of key characters for 10 adult females

CHARACTER			SPECIMEN NO.										$\bar{x}$	σ	$S_{\bar{x}}$
			1	2	3	4	5	6	7	8	9	10			
WHOLE INSECT		Body length(L)	102	90	115	100	85	90	94	85	88	89	1.41mm.	0.14mm.	0.01mm.
HEAD		Prob/Hd.	55/72	55/74	58/82	52/80	52/79	55/80	55/75	55/75	58/75	56/80	0.72	0.04	0.01
		AR	87/59	78/52	78/45	70/52	76/50	72/50	78/50	80/53	73/52	82/54	1.50	0.10	0.03
		PR	13/7.5	14/8.5	14/8	13/8	13/7	13.5/7	14/8.5	13/8	14/8.5	13/7	1.73	0.11	0.04
THORAX	LEGS	Fore TR	44/19	57/23	45/18	46/20	45/19	45/19	52/22	46/18	46/19	46/19	2.41	0.09	0.03
		Mid TR	48/20	50/23	48/20	47/21	47/20	47/20	55/22	49/20	49/21	50/21	2.36	0.08	0.03
		Hind TR	64/24	70/27	61/23	67/26	60/24	64/26	70/27	65/24	62/26	62/27	2.53	0.13	0.04
		Tib.spines	7	7	7	7	7	7	8	8	7	7	7.20	0.42	0.13
	WING	L	59	64	58	59	56	59	59	57	58	59	0.88mm.	0.07mm.	0.02mm.
		W	27	27	27	28	27	29	27	28	27	28.5	0.41mm.	0.004mm.	0.001mm.
		CR	31/59	36/64	30/58	30/59	29/56	31/59	35/59	30/57	30/58	31/59	0.53	0.02	0.01
		VLR	65/53/115	70/52/126	62/50/118	65/53/122	56/46/105	66/51/120	75/59/135	65/52/120	65/52/119	64/51/120	1.26/1/2.31	0.02/1/0.06	0.01/0.32/0.02
		rs/r_1	74/38	87/42	68/30	75/32	71/32	79/37	84/40	68/30	68/30	79/39	2.16	0.13	0.04
		RR	28/30	28/30	29/30	35/28	31/28	39/20	40/29	35/21	35/21	37/23	1.28	0.30	0.10
		m_{3+4}/cu_1	87/53	101/58	90/48	97/52	100/58	100/57	100/56	85/49	94/52	93/50	1.78	0.02	0.01
ABDOMEN	Smaller Spmth.	L	14	14	15	14	15	15	15	16	14	16	222 μ	11.84 μ	3.75 μ
		W	13	13	14	13	14	14	14	15	13	15	207 μ	11.84 μ	3.75 μ
		Duct L	2.6	2.5	4	2	2.5	2.5	3	2.5	2.5	2.5	40.5 μ	3.00 μ	0.95 μ
	Larger Spmth.	L	17	18	16	15	16	18	18	17	18	17	255 μ	15.81 μ	5.00 μ
		W	16	17	16	14	15	17	17	16	16	16	240 μ	14.15 μ	4.47 μ
		Duct L	3	3	3	3	3	4	3	3	3	3	46.5 μ	4.74 μ	1.50 μ

Table 30a.

Trichohelea nicopina n. sp. - Measurements of key characters for two fourth-instar larvae.

CHARACTER			1	2	$\bar{x}$
WHOLE INSECT	Body length (L)		250	210	3.45 mm.
	Width(W)/Depth(D)		19/18	20/20	1.03
HEAD	Lateral View	HR (L/D)	90/44	90/45	2.02
		OH/v	51/50	45/48	0.98
		qt/ts/sq	21.5/26/21	21/26/20	1.04/1.27/1
	Ventral View	L/W	85/63	85/61	1.37
		tt/ant	21/44	20.5/43	0.48
		qq/eyes	35/37	35/35	0.97
		qq/ss	35/58	35/57.5	0.61
		pp/qq	50/35	50/35	1.43
		ss/uu	58/49	57.5/49	1.18
THORAX	Ant. pseud.	L/W/D	30/38/21	23/45/25	1.18/1.80/1

Table 30b.

Trichohelea nicopina n. sp. - Measurements of key characters for single male and female pupa.

CHARACTER			Female		Male	
			Original	Calculated	Original	Calculated
WHOLE PUPA	L		180	2.70 mm.	152	2.28 mm.
	W		31	0.47 mm.	28	0.42 mm.
	Cph/Abd		68/135	0.50	61/110	0.56
CEPHALO-THORAX	L/W		68/31	2.19	61/28	2.18
	Hd/th	Dorsal a	10/37	0.27	11/35	0.31
		Ventral a	26/54	0.48	29/50	0.58
	Resp. Horn	L/W	52/11	4.73	45/7.5	6.00
		TrL/W	40.5/4	10.13	35/3	11.67
		TrL/HL	40.5/52	0.78	35/45	0.78
		No. sp. pap.	16	16	12	12
ABDOMEN	3rd segt (L/W/D)		18/28/25	1/1.56/1.39	14/21/18	1/1.50/1.29
	Last segt (L/W/D)		69/50/45	1.53/1.11/1	52/44/40	1.30/1.10/1
	Term. proc. (L/W/D)		57/26/17	3.35/1.53/1	47/20/13	3.62/1.54/1
	Sex. proc. (L/W/D)		—	—	22/18/15	1.47/1.20/1

Table 30c.

Trichohelea nicopina n. sp. - Measurements of key characters for single adult male.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		116	1.74 mm.
HEAD	Prob/Hd		34/73	0.47
	AR		75/80	0.94
	PR		15/5.5	2.73
THORAX	Legs	Fore TR	50/19	2.63
		Mid TR	50/19	2.63
		Hind TR	60/19	3.16
		Tib. spines	6	6
	Wing	L	54	0.81 mm.
		W	19	0.29 mm.
		CR	26/54	0.48
		vLR	74/66/114	1.12/1/1.73
		rs/r_1	44.5/28	1.59
		RR	13/18	0.72
		m_{3+4}/Cu_1	85/40	2.13
ABDOMEN (GENITALIA)	L/W	9th stern.	21.5/40	0.54
		9th trg.	25/40	0.63
		Bmr	28.5/12	2.38
		Tmr	26.5/6	4.42
		Aed	17/20	0.85
	Clsp	(b/c/b)	11/18/11	0.61/1/0.61

Table 30d.

Trichohelea nicopina n. sp. - Measurements of key characters for single adult female.

CHARACTER			ORIGINAL	CALCULATED
WHOLE INSECT	Body length (L)		110	1.65 mm.
HEAD	Prob/Hd		35/64	0.55
	AR		100/29	3.45
	PR		14/6.5	2.15
THORAX	Legs	Fore TR	53/18	2.94
		Mid TR	52/17	3.06
		Hind TR	63/20	3.15
		Tib. spines	7	7
	Wing	L	50	0.75 mm.
		W	22	0.33 mm.
		CR	27/50	0.54
		vLR	59/52/101	1.14/1/1.94
		rs/r_1	56/30	1.87
		RR	24/23	1.04
		m_{3+4}/Cu_1	76/45	1.69
ABDOMEN	Smaller spmth	L	16.5	56.93μ
		W	13	44.85μ
	Larger spmth	L	16.5	56.93μ
		W	14	48.30μ

Table 31a.

Trichohelea grandis n. sp. - Measurements of key characters for three fourth-instar larvae.

CHARACTER			1	2	3	$\bar{x}$
WHOLE LARVA	Body length (L)		240	245	285	3.85 mm.
	Width(W)/Depth(D)		16.5/16.5	16.5/13	22/18	1.16
HEAD	Lateral View	HR(L/D)	85/45	85/42	89/43	1.99
		OH/v	42/43	41/42	43/45	0.97
		qt/ts/sq	20/22/15.5	19/21/15	20/23/16.5	1.26/1.40/1
	Ventral View	L/W	82/56	80/60	83/58.5	1.41
		tt/ant	22.5/41	21.5/41	22/41	0.54
		qq/eyes	33/38	32/38	32/39	0.84
		qq/ss	33/51	32/55	32/54	0.61
		pp/qq	44.5/33	46/32	45/32	1.40
		pq/qs/sp	20/14/24	22/15/24	22/16.5/25	1.41/1/1.61
		pp/uu	45/51	45.5/55	47/54	0.86
THORAX	Ant. pseud.	L/W/D	35/42/30	28/50/16	30/45/18	1.71/2.81/1

Table 31b.

Trichohelea grandis n. sp. - Measurements of key characters for single male pupa.

CHARACTER			ORIGINAL	CALCULATED
WHOLE PUPA	L		184	2.76 mm.
	W		27	0.41 mm.
	Cph/Abd		67/137	0.49
CEPHALO-THORAX	L/W		67/27	2.48
	Hd/Th	Dorsal a.	9.5/37	0.26
		Ventral a.	21/58	0.36
	Resp. Horn	L/W	44/8	5.50
		TrL/W	36/3	12.00
		TrL/HL	36/44	0.82
		No. sp. pap.	14	14
ABDOMEN	3rd segt (L/W/D)		16/22/20	1/1.38/1.25
	Last segt (L/W/D)		60/43/44	1.40/1/1.02
	Term. proc. (L/W/D)		84/20/18	4.67/1.11/1
	Sex. proc. (L/W/D)		18/15/10	1.80/1.50/1

Table 31c.

Trichohelea grandis n. sp. – Measurements of key characters for two adult males.

CHARACTER			1	2	$\bar{x}$
WHOLE INSECT	Body length (L)		101	98	1.49 mm.
HEAD	Prob/hd		28/68	30/70	0.42
	AR		71/79.5	71/80	0.89
	PR		12/4.5	—	2.67
THORAX	Legs	Fore TR	46/18	51/19	2.62
		Mid TR	44/19	49/18	2.52
		Hind TR	54/18.5	53/19	2.85
		Tib. spines	6	6	6
	Wing	L	—	53	0.80 mm.
		W	—	18	0.27 mm.
		CR	—	25/53	0.47
		vLR	—	67/60/110	1.12/1/1.83
		rs/r_1	—	45/28	1.61
		RR	—		
		m_{3+4}/Cu_1	—	73/34	2.15
ABDOMEN (GENITALIA)	L/W	9th stern.	20/35	22/40	0.56
		9th trg.	28/35	30/40	0.78
		Bmr	28/10	32.5/11	2.88
		Tmr	26/6	31/6	4.75
		Aed	15/17	16/18	0.89
	Clsp	(b/c/b)	12/17/12	11/17/11	0.68/1/0.68

Table 31d.

Trichohelea grandis n. sp. - Measurements of key characters for two adult females.

CHARACTER			1	2	$\bar{x}$
WHOLE INSECT	Body length (L)		95	--	1.43 mm.
HEAD	AR		56/41	110/71	1.46
	PR		15/7	--	2.14
THORAX	Legs	Fore TR	51/18	37/13	2.84
		Mid TR	50/17.5	38/14	2.79
		Hind TR	60/18	48/15	3.27
		Tib. spines	8	--	8
	Wing	L	53	42.5	0.72 mm.
		W	22	18	0.30 mm.
		CR	28/53	22/42.5	0.52
		vLR	60/54/106	50/42/79	1.15/1/1.92
		rs/r_1	67/32	50/27	1.97
		RR	30/20	22/20	1.30
		m_{3+4}/Cu_1	80/41	72/35	2.00
ABDOMEN	Smaller spmth	L	17	--	58.65μ
		W	13	--	44.85μ
	Larger spmth	L	18	--	62.10μ
		W	14	--	48.30μ

Table 32.

Neoforcipomyia saundersi n. sp. - Range in mm. for body lengths and widths of larval, pupal and adult stadia.

STAGE		NO. MEASURED	RANGE LENGTH	RANGE WIDTH
LARVA	1st instar	65	0.345-0.750	0.083-0.135
	2nd instar	21	0.645-1.380	0.135-0.225
	3rd instar	65	1.110-2.100	0.195-0.315
	4th instar	55	1.440-3.075	0.240-0.435
PUPA	Male	10	1.995-2.325	0.525-0.630
	Female	10	1.800-2.070	0.510-0.585
ADULT	Male	10	1.725-1.890	-
	Female	10	1.410-1.785	-

Table 33.

Neoforcipomyia eques (Johannsen) - Range in mm. for body lengths and widths of larval, pupal and adult stadia.

STAGE		NO. MEASURED	RANGE LENGTH	RANGE WIDTH
LARVA	1st instar	53	0.330-0.720	0.075-0.135
	2nd instar	55	0.585-1.320	0.120-0.180
	3rd instar	13	1.050-1.935	0.150-0.285
	4th instar	17	1.410-2.850	0.240-0.420
PUPA	Male	10	1.800-2.085	0.495-0.585
	Female	10	1.620-1.995	0.480-0.555
ADULT	Male	10	1.575-1.770	-
	Female	10	0.900-1.725	-

Table 34.

Bezzia glabra (Coquillett) - Range in mm. for head and body lengths and widths of larval, pupal and adult stadia.

STAGE	NO. MEASURED	RANGE			
		WHOLE INSECT*		HEAD+	
		Length	Width	Length	Width
LARVA					
1st	5	90-145	4-4.5	39-40	13-14
2nd	24	140-279	4.5-7	58-65	18-20
3rd	48	218-445	6-12.5	86-99	23-30
4th	50	376-751	9-24	126-152	31-42
PUPA					
Male	30	212-256	33-44	-	-
Female	37	240-300	40-51	-	-
ADULT					
Male	26	141-202	-	-	-
Female	25	175-226	-	-	-

* Whole Insect : 1 unit = 0.015 mm.

+ Head : 1 unit = 0.00345 mm.

Table 35.

Palpomyia slossonae (Coquillett) - Range in mm. for head and body lengths and widths of larval, pupal and adult stadia.

STAGE	NO. MEASURED	RANGE			
		WHOLE INSECT*		HEAD+	
		Length	Width	Length	Width
LARVA					
1st	26	80-175	4-7.5	41-44	17-18.5
2nd	13	160-274	6-11	59-64	22-24
3rd	21	220-497	10-19.5	85-94	30-30.4
4th	36	435-896	14-37	130-149	37-55
PUPA					
Male	22	243-300	47.5-57.5	-	-
Female	45	276-390	58-80	-	-
ADULT					
Male	44	150-230	-	-	-
Female	46	221-318	-	-	-

* Whole Insect : 1 unit = 0.015 mm.

\+ Head : 1 unit = 0.00345 mm.

Table 36.

Dasyhelea grisea (Coquillett) - Range in mm. for head and body lengths and widths of larval, pupal and adult stadia.

STAGE	NO. MEASURED	RANGE			
		WHOLE INSECT*		HEAD+	
		Length	Width	Length	Width
LARVA					
1st	13	40-75	3.5-5.5	31-33	17.5-18
2nd	23	69-128	5.5-9.0	47-50	24-26.5
3rd	23	114-205	8.0-15.0	69-75	35-39
4th	10	180-300	13.5-20.0	95-106	50-57
PUPA					
Male	11	141-195	28-36	-	-
Female	12	142-205	29-35	-	-
ADULT					
Male	5	129-146	-	-	-
Female	6	105-128	-	-	-

* Whole Insect : 1 unit = 0.015 mm.

\+ Head : 1 unit = 0.00345 mm.

Table 37.

Neoforcipomyia saundersi n. sp. - Duration in days of stadia of field-collected immature stages developing on moist, decaying wood with a covering of algae and moss at room temperature and humidity. (70°F. and 50% R.H.)

STAGES	NO. OF SPECIMENS	DURATION IN DAYS		$\bar{x}$ DAYS FROM EGG-HATCHING TO ADULT EMERGENCE
		$\bar{x}$	Range	
LARVAE				18.3
1st	30	3.3	1.5-7.0	
2nd	60	2.5	1.0-5.0	
3rd	84	2.9	1.0-11.0	
4th	79	5.5	2.5-12.5	
PUPAE				
Female	36	4.2	3.0-5.0	
Male	39	4.2	3.0-6.0	

Table 38.

Neoforcipomyia eques (Johannsen) - Duration in days of stadia of field-collected immature stages developing on moist, decaying wood with a covering of algae and moss at room temperature and humidity. (70°F. and 50% R.H.)

STAGES	NO. OF SPECIMENS	DURATION IN DAYS		$\bar{x}$ DAYS FROM EGG-HATCHING TO ADULT EMERGENCE
		$\bar{x}$	Range	
LARVAE				
1st	56	6.9	4.0-10.0	33.0
2nd	59	6.5	2.0-12.0	
3rd	55	4.9	2.0-13.0	
4th	53	8.2	2.5-16.0	
PUPAE				
Female	29	6.7	5.5-8.0	
Male	39	6.6	4.5-8.5	

Table 39.

Bezzia glabra (Coquillett) - Duration in days of stadia of field-collected immature stages developing in blanket algae on chironomid and *Dasyhelea grisea* larvae and pupae at room temperature and humidity. (70°F. and 50% R.H.)

STAGES	NO. SPECIMENS	DURATION IN DAYS		$\bar{x}$ DAYS FROM EGG-HATCHING TO ADULT EMERGENCE
		$\bar{x}$	Range	
LARVA				64.7
1st	1	8	8	
2nd	6	14.3	14.3	
3rd	5	24.4	16-35	
4th	7*	15.7	11-19	
PUPA				
Female	15	2.3	1.5-3.5	
Male	8	2.3	1.5-2.5	

* These belong to a minority; the majority overwinters.

Table 40.

Palpomyia slossonae (Coquillett) - Duration in days of stadia of field-collected immature stages developing in blanket algae on chironomid and *Dasyhelea grisea* larvae and pupae at room temperature and humidity. (70°F. and 50% R.H.)

STAGES	NO. SPECIMENS	DURATION IN DAYS		$\bar{x}$ DAYS FROM EGG-HATCHING TO ADULT EMERGENCE
		$\bar{x}$	Range	
LARVA				$\doteq$ 365
1st	20	14.25	10-19	
2nd	19	14.26	10-22	
3rd	16	35.19	7-58	
4th	-	-	-	
PUPA				
Female	20	3.78	2-5	
Male	10	4.05	3-5	

Table 41.

Dasyhelea grisea (Coquillett) - Duration in days of stadia of field-collected immature stages developing in and on blanket algae and debris at room temperature and humidity. (70°F. and 50% R.H.)

STAGES	NO. SPECIMENS	DURATION IN DAYS		$\bar{x}$ DAYS FROM EGG-HATCHING TO ADULT EMERGENCE
		$\bar{x}$	Range	
LARVA				30.3
1st	91	7.5	4-13	
2nd	126	6.5	4.5-15.5	
3rd	203	6.5	4.5-18	
4th	194	7.3	5.5-22	
PUPA				
Female	78	2.5	1.5-3.5	
Male	79	2.5	1.5-3.5	

EVOLUTIONARY DEVELOPMENT OF CLASPETTES IN THE DASYHELEINAE AND CERATOPOGONINAE

A. DASYHELEINAE

In the Dasyheleinae the evolutionary development of the claspettes begins with the 'third' stage of the Atrichopogon prototype condition (Fig. 40a, A_3) and proceeds in three trends: A, B and C (Fig. 40a). In trends A and B, the hook-shaped claspettes rise above their bases and meet apically either sharply or in a square-top. The claspette processes are then produced from the left or the right basal arm. Further developments, as shown in the diagram, are self-explanatory. In trend C, the claspettes meet without rising above the level of the hook-shaped basal arms but at the level or below that of the basal arms as shown,

Trends A and B may also begin with the second Atrichopogon prototype stage (A_2) and proceed in exactly the same way as shown for A_3.

B. CERATOPOGONINAE

In the Culicoidini and Ceratopogonini (Fig. 40b, trends A, B and C), evolutionary development of the claspettes begins with the hypothetical cases as shown. In trend A, the short basal arms of the first stage Atrichopogon prototype condition (A_1) give rise to claspette processes from their apices. These processes elongate and become variously modified as shown. In trends B and C the claspette processes arise from the recurved apices of the apical arms and become elongated and variously modified as shown.

In the rest of the Ceratopogoninae (trend D) claspette processes are produced from the inner basal corners of the basal arms. These

Fig. 40a. Evolutionary trends in the development of claspettes in the Dasyheleinae

A_3 -- *Atrichopogon boharti* Tokunaga (1962)

1 -- *Dasyhelea pelilliouensis* Tokunaga (1940)

2 -- *Dasyhelea luteicauda* Tokunaga (1962); *D. gressitti* Tokunaga (1959); *D. flavibasalis* Tokunaga (1940); *D. palouensis* Tokunaga (1940); *D. carolinensis* Tokunaga (1941); *D. perfida* Johannsen (1931); *D. subperfida* Tokunaga (1940); etc.

3 -- *Dasyhelea fumala* Tokunaga (1940)

4 -- *Dasyhelea cincta* (Coquillett) (1901); *D. robustiforceps* Tokunaga (1962); etc.

5 -- *Dasyhelea flavescens* Tokunaga & Murachi (1959); *D. subscutellata* Tokunaga (1940); *D. palloris* Tokunaga & Murachi (1959); etc.

6 -- *Dasyhelea truncata* Tokunaga & Murachi (1959)

7 -- *Dasyhelea ryukyuensis* Tokunaga (1962); *D. sabroskyi* Tokunaga (1959); *D. insularis* Tokunaga (1940); etc.

8 -- *Dasyhelea yoshimurai* Tokunaga (1940)

9 -- *Dasyhelea symmetria* Tokunaga (1962); *D. parvistylata* Tokunaga & Murachi (1959); *D. pallivittae* Tokunaga (1959); *D. nigrovis* Tokunaga & Murachi (1959); etc.

10 -- *Dasyhelea nigristigmata* Tokunaga & Murachi (1959); *D. esakii* Tokunaga (1940); etc.

11 -- *Dasyhelea sagittifera* Tokunaga & Murachi (1959); etc.

12 -- *Dasyhelea flavicaudalis* Tokunaga & Murachi (1959); *D. raripilosa* Tokunaga (1940); *D. quaternihamata* Tokunaga (1959); etc.

13 -- *Dasyhelea dupliforceps* Tokunaga (1959);

14 -- *Dasyhelea furcillifera* Tokunaga (1959); etc.

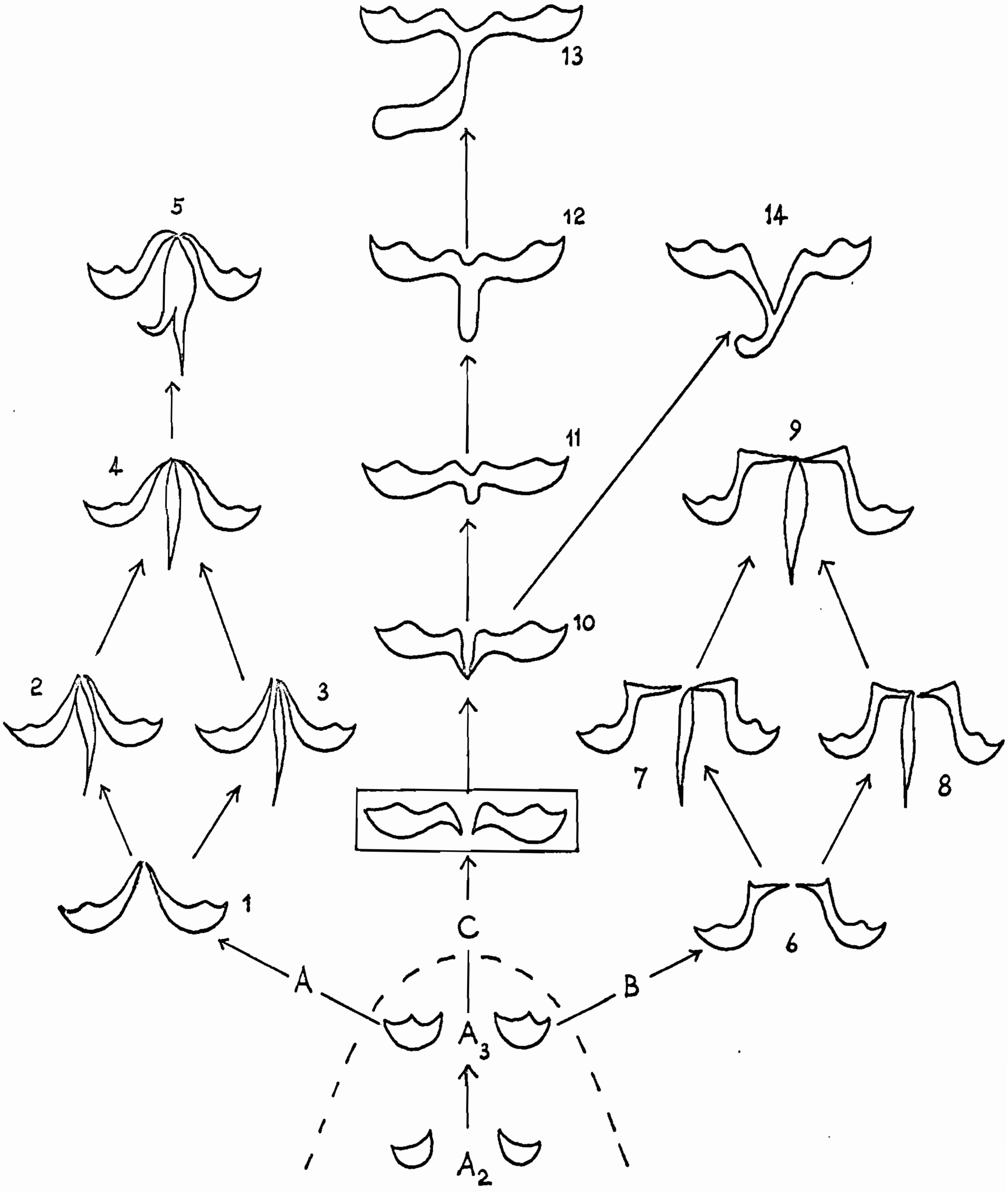


Fig. 40a. Evolutionary trends in the development of claspettes in the Dasyheleinae

Fig. 40b. Evolutionary trends in the development of claspettes in the Ceratopogoninae

1 -- *Culicoides brookmani* Wirth (1952); *C. chiopterus* (Meigen) (1820); *C. guttifer* (de Meijere) (1907); *C. okinawensis* Arnaud (1956); *C. cockerellii saltonensis* Wirth (1952); etc.

2 -- *Culicoides jamesi* Fox (1946)

3 -- *Culicoides hieroglyphicus* Malloch (1915)

4 -- *Culicoides stonei* James (1943); *C. loughnani* Edwards (1922); *C. palmerae* James (1943); *C. canithorax* Hoffman (1925); *C. biguttatus* (Coquillett) (1901); *C.* (*Trithecoides*) spp. etc.

5 -- *Culicoides inamollae* Fox & Hoffman (1944)

6 -- *Culicoides variipennis* (Coquillett) (1901); *C. peliliouensis* Tokunaga (1936); etc.

7 -- *Culicoides sabroskyi* Tokunaga (1959)

8 -- *Alluaudomyia insulicola* Tokunaga & Murachi (1959)

9 -- *Alluaudomyia monopunctata* Tokunaga & Murachi (1959)

10 -- *Culicoides denningi* Foote & Pratt (1954)

11 -- *Culicoides tenuistylus* Wirth (1952)

12 -- *Ceratopogon culicoidithorax* Hoffman (1926)

13 -- *Alluaudomyia needhami* Thomsen (1935); *Palpomyia tibialis* (Meigen); etc.

14 -- *Alluaudomyia bipunctata* Tokunaga & Murachi (1959); etc.

15 -- *Alluaudomyia bella* (Coquillett) (1902); etc.

16 -- *Alluaudomyia spinosipes* Tokunaga (1962)

17 -- *Stilobezzia gressitti* Tokunaga & Murachi (1959); *S. fuscigenua* Tokunaga & Murachi (1959); etc.

18 -- *Serromyia femorata* (Meigen)

19 -- *Neurohelea nigra* Wirth (1952); etc.

20 -- *Monohelea macfiei* Wirth (1953)

21 -- *Monohelea johannseni* Wirth (1953)

22 -- *Palpomyia serripes* Meigen (1818); *Clinohelea usingeri* Wirth (1952); etc.

Fig. 40b. Evolutionary trends in the development of claspettes in the Ceratopogoninae

23 -- *Jenkinshelea corea* de Meijere

24 -- *Palpomyia flaviceps* (Meigen) (1804); *Bezzia setulosa* (Loew) (1861); *B. bivittata* (Coquillett) (1905); *B. badiifemorata* Tokunaga & Murachi (1959); *B. maculifemorata* Tokunaga & Murachi (1959); etc.

25 -- *Sphaeromias longipennis* (Loew) (1861)

26 -- *Palpomyia linsleyi* Wirth (1952); *P. armatipes* Wirth (1952); *Bezzia punctipennis* (Williston) (1896); etc.

27 -- *Stilobezzia okinawensis* Tokunaga (1962)

28 -- *Monohelea palauensis* Tokunaga (1959); *Stilobezzia* (*Neostilobezzia*) *unifascidorsalis* Tokunaga (1959); etc.

29 -- *Stilobezzia spadicitibialis* Tokunaga & Murachi (1959); *S. fusiscutellata* Tokunaga & Murachi (1959); *S.* (*Neostilobezzia*) *calcaris* Tokunaga & Murachi (1959); *S. abdominalis* Tokunaga & Murachi (1959); etc.

30 -- *Stilobezzia* (*Neostilobezzia*) *tenuiforceps* Tokunaga & Murachi (1959); *Stilobezzia fusistylata* Tokunaga & Murachi (1959); *S. spadicicoxalis* Tokunaga & Murachi (1959); *S. suboror* Tokunaga (1941); *S. fulviscuta* Tokunaga & Murachi (1959); etc.

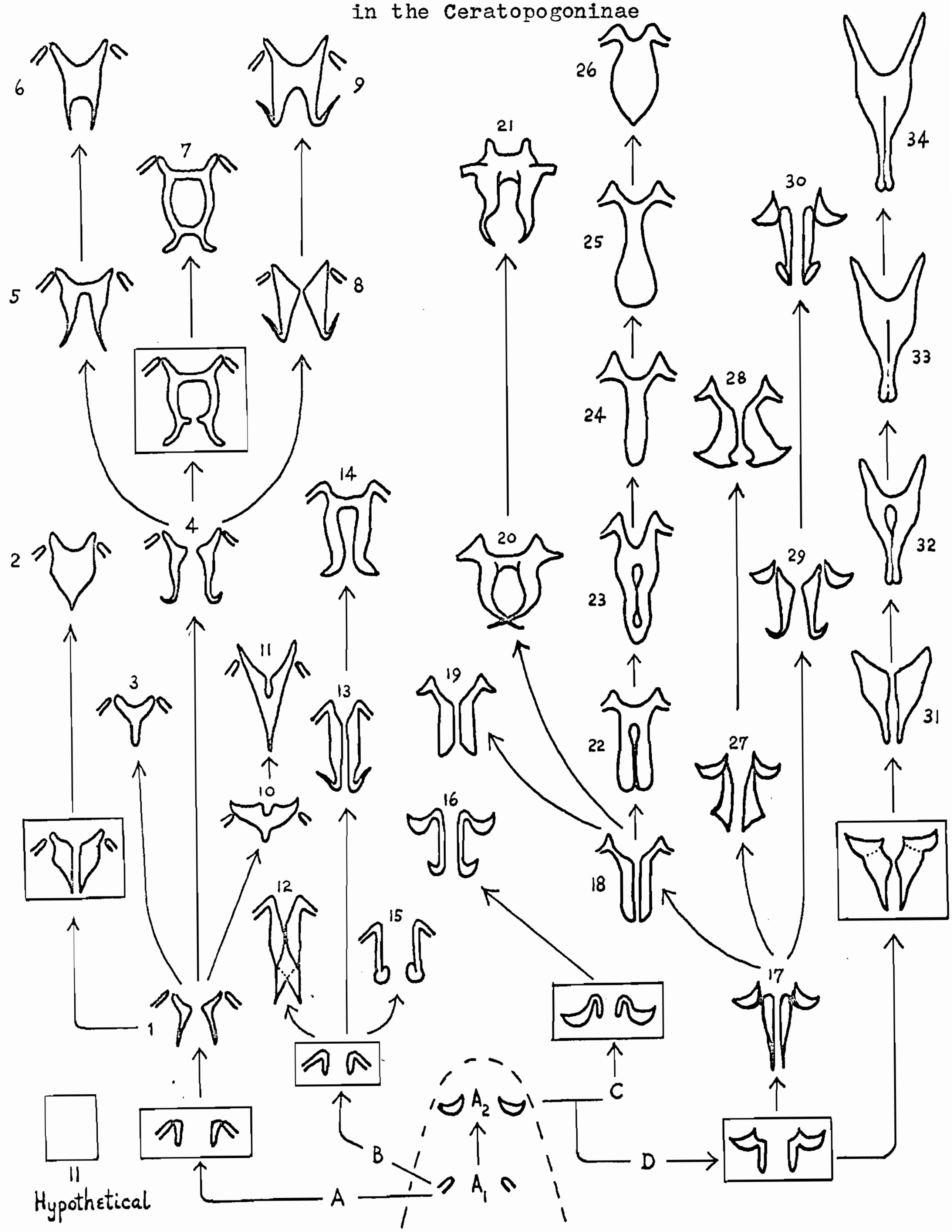
31 -- *Johannsenomyia sybleae* Wirth (1952)

32 -- *Mallochohelea caudelli* (Coquillett) (1905); *M. albibasis* (Malloch) (1915); etc.

33 -- *Mallochohelea albihalter* Wirth (1962)

34 -- *Mallochohelea smithi* (Lewis) (1956)

Fig. 40b. Evolutionary trends in the development of claspettes in the Ceratopogoninae



processes become elongated and remain separate but take on various shapes or become fused in various ways, as shown.

From the evolutionary development of the claspettes it would appear that the Ceratopogon group is intermediate between the Culicoidini and the other Ceratopogonine tribes but much closer to the Culicoidini. It would also appear that the Sphaeromiini and the Palpomyiini are closer to each other than to the other tribes and similarly for the Heteromyiini and the Stilobezini. Wirth's (1962) reclassification of the Palpomyia-Bezzia-Macropeza Groups (Ann. Entomol. Soc. Am. 55: 272-287) seems fairly sound but when based on male genitalic characters, many of the genera in these groups are not clear-cut, due to overlap in these characters. A revision of these higher Ceratopogoninae, especially from comparative morphology of all stages, with special emphasis on the male genitalia, is, in the opinion of the writer, very desirable and should be attempted.

THE SYSTEMATIC POSITION OF THE GENUS PARADASYHELEA MACFIE (1940)

As pointed out by Wirth and Lee (1959) (Bull. Brooklyn Entomol. Soc. 54(4): 114-121) the genus Paradasyhelea resembles "(a) Forcipomyia in the vestiture of the wings, oblique r-m cross vein, hairy scutellum, broadly separated eyes, tarsal ratio (hind T_1/T_2) less than 2, presence of scattered, slender, hyaline sensory pegs on antenna, and structure of male gonostyles and parameres; (b) Dasyhelea in the four-segmented palpus, hairy eyes, short proboscis with rudimentary mouthparts, basal verticils present on all of segments three to fifteen, male antenna with last four segments elongated, vestigial empodium, and the shape of apicolateral processes of male genitalia; (c) Culicoides in the presence of well-developed humeral pits, presence of distal, minute sensory pits bordered by fine setae on certain antennal segments, distal antennal segment without terminal nipple, and Y-shaped aedeagus."

According to Wirth & Lee (loc. cit.) only four species have been known and of the immature stages only the pupa has been collected.

Based on adult characters, particularly those of the wing and male genitalia, Paradasyhelea might be placed in the Forcipomyiinae. Its Y-shaped aedeagus, typical of Culicoides, shows that it has evolved a stage beyond the typical Forcipomyian shield-shaped type of aedeagus. The structure of the claspettes would place it close to Caloforcipomyia. However, present knowledge from all stages, does not justify its inclusion in the Forcipomyiinae but suggests that it should be placed between the Forcipomyiinae - Dasyheleinae stem and the Ceratopogoninae stem, and that a new subfamily "Paradasyheleinae" should be erected to accommodate the four known species.