ON THE WING-VENATION OF *CHAETEESSA* AND OTHER MANTIDS (INSECTA : MANTODEA)

BY

JOHN SMART, M.A., D.Sc., F.Z.S.

Department of Zoology, University of Cambridge

[Accepted October 9th, 1956]

(With 1 plate and 4 figures in the text)

CONTENTS

INTRODUCTION

Ragge (1955) states that " No work on the tracheation of Mantoid [*sic*] nymphal wing-pads and no detailed work on the adult venation has apparently been done in the past ". In a tabular statement of the way in which a number of workers have differed in their application of the Comstock-Needham notation of vein nomenclature to the wings of mantids he amply justifies this statement.

Ragge (1955) gives an account of the venation of mantids based on examination of the nymphal wing-pads of *Ameles* and *Sphodromantis* and the wings of *Ameles, Sphodromantis, Bolbena, Empusa* and *Rivetina*. Ragge, whose main interest was the venation of Saltatoria, concluded that there " are a number of venational features which are common to both Blattoidea and Mantoidea ".

When investigating the wing-venation of the American Cockroach (*Periplaneta americana* L.) (Smart, 1952) and the Migratory Locust (*Locusta migratoria* L.) (Smart, 1953 c) the wing-venation of a number of mantids and of the tracheation of some nymphal wing-pads were examined and found to confirm Ragge's findings as to the condition of the venation in the more highly evolved members of the group such as Ragge was in fact examining. However, the writer endeavoured to find out which mantids could be considered the most primitive on grounds other than wing-venation.

The classification of the mantids has not yet reached stability. Most writers follow Giglio-Tos (1927) to a varying extent. He divided the group (then designated as the Family Mantidae of the Order Orthoptera) into thirty-two subfamilies. Handlirsch (1930) realised the exceptional features of

Chaeteessa and placed the genus in a family of its own at the beginning of his classification thus :—

Fam. Chaeteessidae : *Chaeteessa* (Neotropical).
Fam. Mantoididae :
Sub-fam. Mantoidinae : *Mantoida* (Neotropical).
Sub-fam. Metallyticinae : *Metallyticus* (Malayan).
Sub-fam. Eremiaphilinae : *Eremiaphila* (Palaeartic)
and thirteen other sub-families comprising all the remaining genera of Mantids.

Handlirsch (1930) figured *Chaeteessa* and the wing of *Metallyticus* without showing sufficient detail for fully appraising the primitive or otherwise condition of the wings.

Chopard (1949) gives a brief conspectus of classification of mantids. He does not adhere closely to Giglio-Tos (1927) or Handlirsch (1930) but divides the group up into thirteen families. Chopard does not mention *Chaeteessa* in the systematic part of his work which has no family (or other segregate) comparable to Handlirsch's Chaeteessidae. *Mantoida* is placed in Chopard's second family Mantoididae ; and *Metallyticus* is in a family Metallyticidae. Preceeding both these families at the beginning of his classification is a family Amorphoscelidae. Chopard suggests, however, that the Amorphoscelidae may be a polyphyletic group united by the possession of feebly armed fore-legs ; he does not give a list of genera comprised in the family but from the text it may be inferred that it contains *Amorphoscelus*, *Perlamantis* and *Paraoxypilus*. He would perhaps include the *Chaeteessa* in the Amorphoscelidae. It may be noted that the feebly armed fore-leg of *Amorphoscelus* is obviously specialised and not primitive.

As now restricted, the subfamily Eremiaphilinae comprises only forms that are brachypterous, have well armed fore-legs and live under arid conditions.

In discussing the wing-venation the Comstock-Needham venation nomenclature as modified by Snodgrass (1935) will be used as in my previous papers on wings of *Periplaneta* (Smart, 1952), *Physemacris* (Smart, 1953 a), *Dissosteira* (Smart, 1953 b) and *Locusta* (Smart, 1953 c). Ragge (1955), used the original Comstock-Needham terminology for perfectly valid reasons of convenience ; in the writer's above-mentioned papers, preference was made of Snodgrass's modifications for the reasons stated (Smart, 1952) especially the individuality of Postcubitus of Snodgrass. Thus Pcu (Postcubitus) of my papers would be Ragge's 1An (First Anal) and my 1V his 2An (Second Anal). The conventional abbreviations for names of veins will be used and a list of these abbreviations is contained in the legend to Fig. 1. Except where it is specifically mentioned the named veins conform to Snodgrass's definitions (1935) in respect of articulation, etc., at the wing-base in so far as this could be ascertained in the dried specimens available.

CHAETEESSA

The fore-leg (Pl., fig. 1) shows the following features that are probably primitive :—1. Tarsi and foot of proportions, in relation to tibia and femur, that make it probable that the leg can function in normal manner in spite

of obvious raptorial adaptation of tibia and femur ; more evolved mantids have tarsi and foot looking like a mere appendage of raptorial tibia. 2. Tibio-tarsal articulation apical on tibia ; more evolved mantids have it sub-terminal and the distal end of the tibia projects beyond articulation as a hook or claw. 3. Both the tibia and femur have two rows of spines, each row fairly evenly developed and not a very great degree of difference between the rows, except one row on the femur is larger than others ; more evolved mantids have very varied conditions of development of the spines on the tibia and femur.

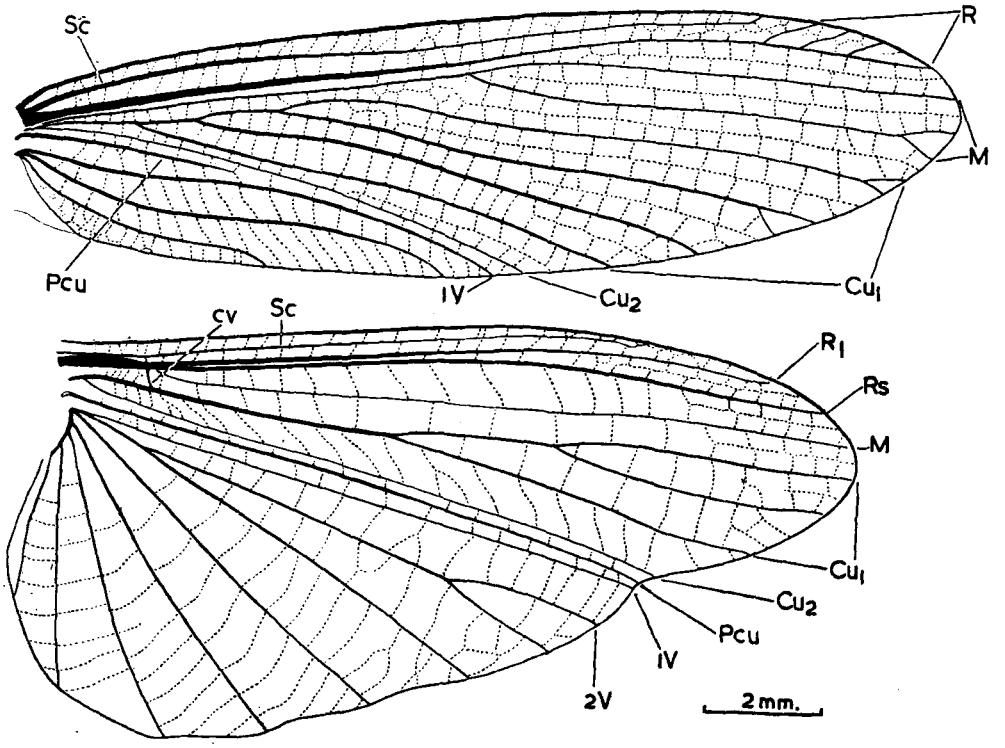


Fig. 1. Wings of *Chaeteessa filata* Burm. Venation labelled with Snodgrass's modified Comstock-Needham nomenclature.

C= Costa ; Sc= Sub-Costa ; R= Radius ; Rs= Radial Sector ; Rl= First branch of Radius ; M= Media ; Cu= Cubitus ; Cul= First branch of Cubitus ; Cu2= Second branch of Cubitus ; Pcu= Postcubitus (Snodgrass's term for First Anal Vein of Comstock & Needham) ; 1V= First Vannal vein (Snodgrass's term for Second Anal of Comstock & Needham) ; 2V= Second Vannal Vein (Snodgrass's term for Third Anal of Comstock & Needham) ; cv= distinctive cross-vein mentioned in text.

The wings (Pl., fig. 2 ; text-fig. 1) are membraneous and both of similar texture. C, developed in both wings ; no pre-costal area. Sc, simple and unbranched, runs well beyond mid-point of wing before joining C. Cross-veins well developed, fairly regular in arrangement. Areas between Sc and C, and Sc and R, narrow in both wings with, except here and there, but a single row of cells.

The fore-wing has R with a few small but definite apical antero-pectinate branches reminiscent of antero-pectinate branched R of such a blattid fore-wing as *Periplaneta*. R convex throughout its length.

M is weak as in *Periplaneta* and other blattids with a single furcation just distal to mid-point of wing ; stem of M concave and completely independent of R right to wing articulation. Both branches of M become convex with concave intercallary vein developed among a double row of cells formed by cross-veins between them, and between them and R in front and Cul behind. Posterior branch of M has terminal furcation.

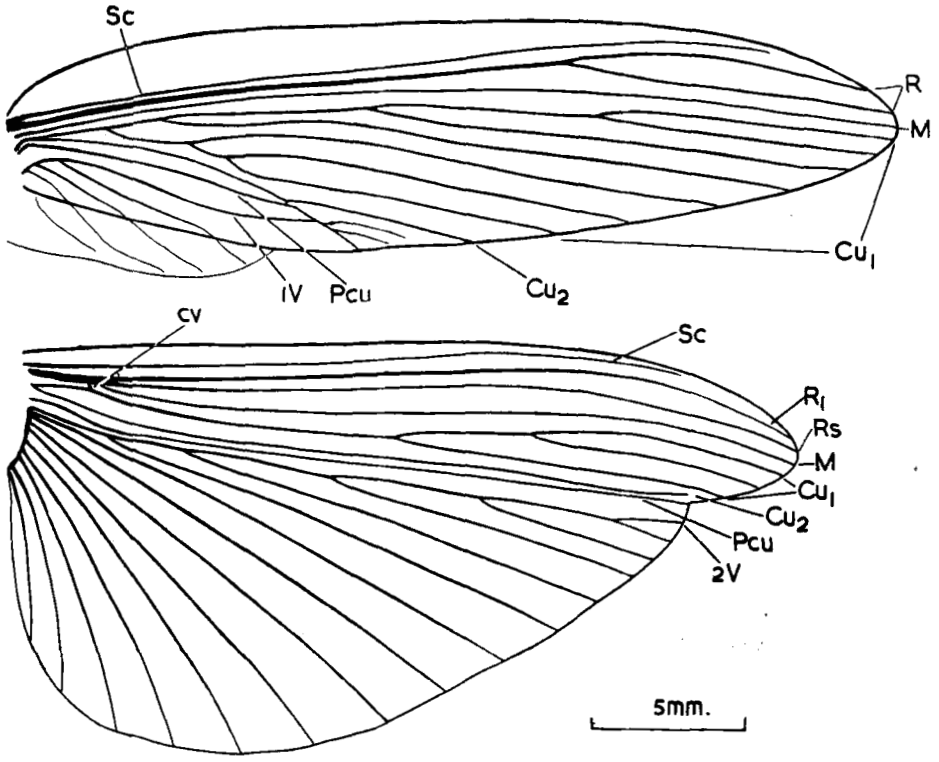


Fig. 2. Wings of *Mantis religiosa* Linn. ; Cross-veins omitted. (See Fig. 1 for explanation of venation symbols).

Cu arises independently at base of fore-wing and forks immediately into branching, strongly convex, Cul and much weaker, simple unbranched, concave Cu2. All four branches of Cul remain convex with concave intercallary veins forming between them. Branches of Cul and intercallaries, except most posterior, have terminal furcations.

Condition of Cul is intermediate between that of *Periplaneta* and other blattids, where it is many branched in a somewhat irregular postero-pectinate manner, and *Locusta* and most other acridids where it is three-branched.

Cu2, marking off vannus from remigium is simple, unbranched, weakly developed and concave. Cross-veins connecting Cu2 with Pcu (proximally)

and 1V (distally) behind are evenly sclerotised. Cross-veins connecting Cu2 with Cul or its most posterior branch in front have sclerotisation weakened just before cross-veins contact Cu2. This is reminiscent of line of weakness in tegmena of *Periplaneta* and *Locusta* which Smart (1952, 1953 c) suggested acted as a hinge to allow adjustment of remigium and vannus in relation to each other in flight. In *Periplaneta* and *Locusta*, however, line of weakness is posterior to Cu2.

Pcu a short convex vein that fails to reach half-way to wing-margin is reminiscent of *Periplaneta*.

Three vannal veins present. Cross-veins fall away from 1V and 2V in distinctive postero-pectinate manner, quite unlike multi-branched V of *Periplaneta* or single straight 1V of *Locusta*.

Small jugal lobe (not seen in Fig. 2 of the plate because it is folded under vannus) has an irregular net of very weak veins on it.

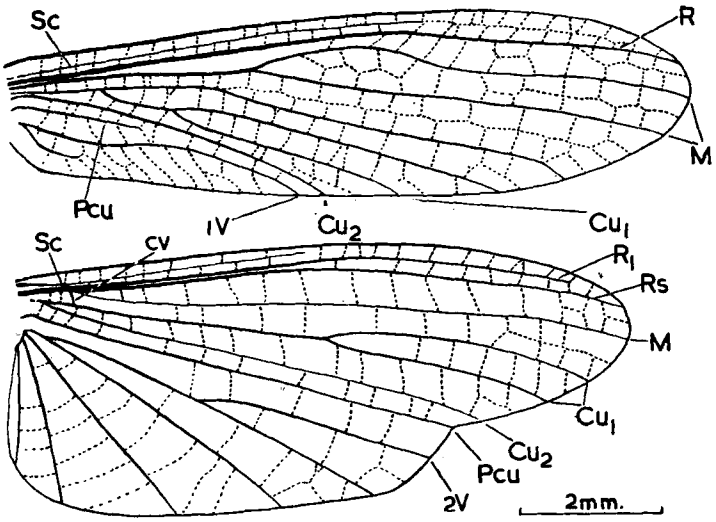


Fig. 3. Wings of *Miomantis* sp. (See Fig. 1 for explanation of venation symbols).

The hind-wing is, at first sight, reminiscent of Plecoptera owing to the pattern of cross-veins between Cul and Cu2. In Text-fig. 1 veins R and M are labelled in accordance with Ragge's (1955) interpretation of mantid venation. R and M form a complex common stem towards the base of wing though this appears (Pl., fig. 2) to be two veins in close apposition rather than a complete fusion into one large vein. R1 appears to run directly from wing-base as a single strong convex vein. Alongside of R1, and in fact apparently tucked partly beneath it, i.e. concave in relation to R1, there appears to be a second vein which gives off a distinctive, strong, convex, rather oblique cross-vein (cv), and then forks to form simple Rs and simple M. At its origin Rs is concave in relation to R1 but as Rs runs out into the wing-field it becomes convex.

M is a weakly developed concave vein which becomes convex distally where concave intercallary veins form between it and Rs in front and Cul behind.

This interpretation of the venation in *Chaeteessa* for these various veins labelled R1, Rs and M is accepted for two reasons. Firstly, this is correct succession for the various veins in the Comstock-Needham system as adopted by Ragge (1955) and it "fits" the wing of *Chaeteessa*. Secondly, Ragge has shown that in the mantids he examined the trachea of this vein Rs in nymphal wing-pad is a branch of trachea coming along R, giving rise to trachea of R1. My own examination of nymphal wing-pads confirms this.

The vein now labelled Rs has, however, some slightly unusual features for a radial sector. (1). It appears to be more closely associated with M at the wing base than with R1 (Pl., fig. 2). (2). The fore-wing shows primitive antero-pectinate branched R and no trace of sector formation which makes the advanced condition in the hind wing with long Rs forking from stem near the wing-base surprising. (3). In most orthopteroid insects where R forks into distinct R and Rs this furcation is well away from the wing-base. (4). In many orthopteroids M develops into a distinctive two-branched form.

In the imaginal hind-wing of *Chaeteessa* it would be possible to regard R1 as a simple convex R that had lost even remnants of the antero-pectinate branching found in the fore-wing and then to consider Rs with its apparent independence from R1, as a convex Anterior Media in Lameere's (1922) sense. The vein now labelled M would then become a simple concave Posterior Media in this sense. This interpretation would explain the unusual features already mentioned.

Smart (in press) points out that the tracheae of nymphal wing-pads cannot be relied upon entirely as completely homologous with the imaginal venation, but only as a useful guide to it. It is conceivable that a branch of M might fuse with R, and, loosing its original tracheation become retracheated by a new branch trachea arising from the main trachea of R. Such switching of tracheation is found as individual variation in the nymphal wing-pads of *Periplaneta*.

Specimens of *Chaeteessa* are rare in collections and nymphal material seems unknown. It would therefore seem best, for the time being at least, to apply Ragge's (1955) interpretation of the mantid R and M since it fits.

Cu forks at the base of the hind-wing. Cul, strongly convex, with three branches ; terminal furcations and intercallary veins relatively weakly developed compared with the fore-wing. Line of weakness along cross-veins at the plical fold immediately behind Cu2.

Cu2 a weak, concave, unbranched vein. Cross-veins between Cul and Cu2 strongly developed ; undirectional slant gives the impression of Plecoptera wing. In both *Periplaneta* and *Locusta* Cu2 is weak and in the latter without a corresponding fully developed trachea in the nymphal wing-pad. The wing-pads of nymphs of higher mantids observed by Ragge (1955) and myself have this vein tracheated.

Pcu, unlike same vein in the fore-wing, well developed and reaching wing-margin ; cross-veins reach it from both sides.

1V simple, 2V branched, subsequent vannal veins simple, no intercallaries developed. Vannus in *Chaeteessa* thus more like that of *Periplaneta* than *Locusta*. Distinct cross-veins reach 1V from Pcu in front and 2V behind.

OTHER MANTIDS

The writer has examined wings of a number of other mantid genera (Text-figs. 2, 3, 4) and a few nymphal wing-pads. In addition to specimens of more obviously specialised and highly evolved genera, the wings of *Metallyticus*, *Mantoida*, *Amorphoscelus*, *Paraoxypilus*, *Gyromantis*, *Phthersigena* and several other small mantids that gave a superficial impression of non-specialised structure were examined. Specimens of *Perlamantis* were not available but a species has been well figured by Chopard (1943). From the literature, the

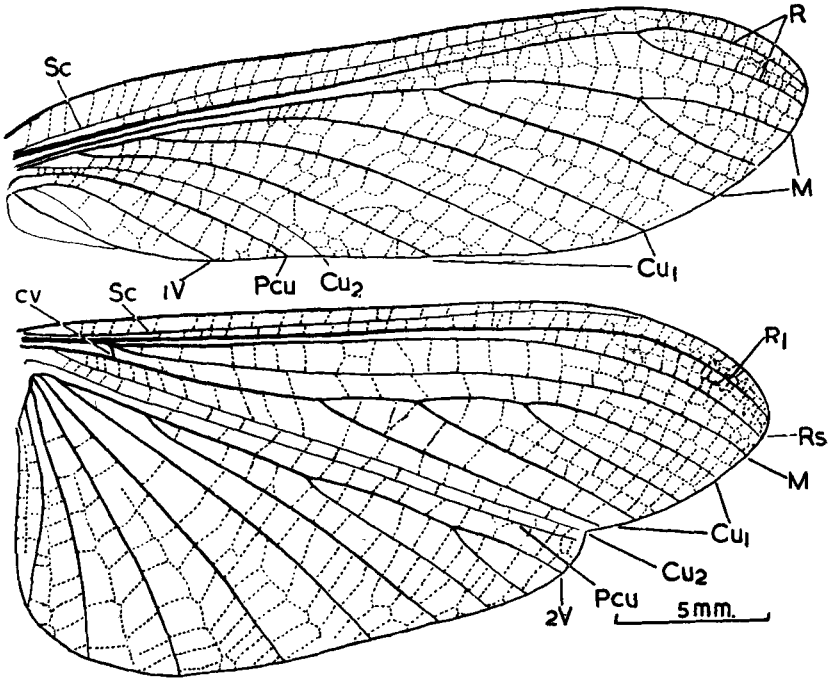


Fig. 4. Wings of *Mantoida sp.* (See Fig. 1 for explanation of venation symbols).

genera named above might be expected to show primitive structure of one kind or another. However, *Metallyticus* alone has a wing-venation that calls for special comment. All the other genera have venations directly comparable to that of the more evolved forms such as Ragge (1955) considered and figured.

The wings of mantids, excluding for the moment *Chaeteessa* and *Metallyticus*, range from the simple membraneous kind with a net of simple, regular, cross-veins to forms in which the fore-wings are heavily sclerotised and of peculiar shapes and sizes apparently adapted for purposes of leaf-mimicry and enemy-frightening. Many mantids are brachypterous or even apterous. Throughout all these forms venation is similar to that described by Ragge

(1955) in fundamentals. Certain main longitudinal veins may have a greater or lesser number of ultimate branches. Inter-vein spaces that are increased in area, such as that between C and Sc in wings of many leaf mimics, may have the space filled up with an anastomosing net of small veins arising from cross-veins which branch in an arborescent manner. Where the fore-wings become sclerotised there is no trace of the lines of weakness noted in *Periplaneta* (Smart, 1952) or *Locusta* (Smart, 1953 c).

Uniformity of venation and features such as absence of lines of weakness in sclerotised tegmina may, perhaps, be explained by the tendency of mantids to disuse powers of flight.

When the wing-venation of these various mantids (Text-figs. 2, 3, 4) is compared with that of *Chaeteessa* two things are most noticeable. Firstly, they show no traces of antero-pectinate branching of R but instead have R in a condition that can be interpreted in terms of R1 with a posteriorly divergent Rs (see Ragge, 1955). Secondly, the first vein immediately posterior to the readily recognisable Pcu (=Ragge's 1A) in the hind-wings is a branching vein (Ragge's 2A) whereas in *Chaeteessa* there is a simple straight vein 1V between Pcu and the branching 2V (=Ragge's 2A) as in *Periplaneta* (Smart, 1952). At first sight one would have the impression that 1V in *Chaeteessa* is simple and unbranched while in the others it is branched.

Examination of the wings of *Metallyticus* convinces me that the true 1V of the hind-wings of *Chaeteessa* and *Periplaneta* is in fact lost in these higher mantids and that branching vannal veins are homologous in all mantids and should be called 2V even when the vein immediately in front of them is a clearly recognisable Pcu.

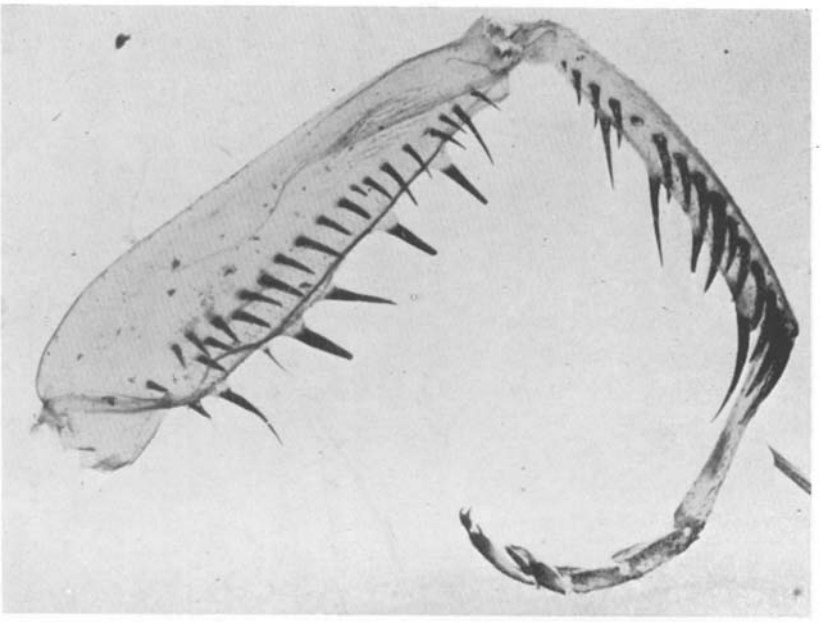
Metallyticus is almost unique among mantids and Chopard (1949) raised the segregate comprising it to family rank. Were it not for the fore-legs and head, species of *Metallyticus* might be taken for dark, metallic coloured cockroaches. The fore-wings are sclerotised and there is a multiplication of longitudinal veins reminiscent of those in tegmen of the cockroach ; R in the fore-wing and Rs in the hind-wing have traces of antero-pectinate branching very similar to that seen in *Chaeteessa*. In the hind-wing there is a weak, simple, concave, 1V between Pcu and branching 2V, as in *Chaeteessa*. This simple unbranched 1V does not reach the margin of the wing. It is however a true vein and not a fold or thickening in the wing-membrane as is proved by the fact that faint cross-veins reach it from Pcu in front and 2V behind at irregular intervals ; when cross-veins pass over a fold or simple thickening in the wing-membrane in their passage from one vein to another they run directly through fold and this condition can be detected at once.

Conclusions

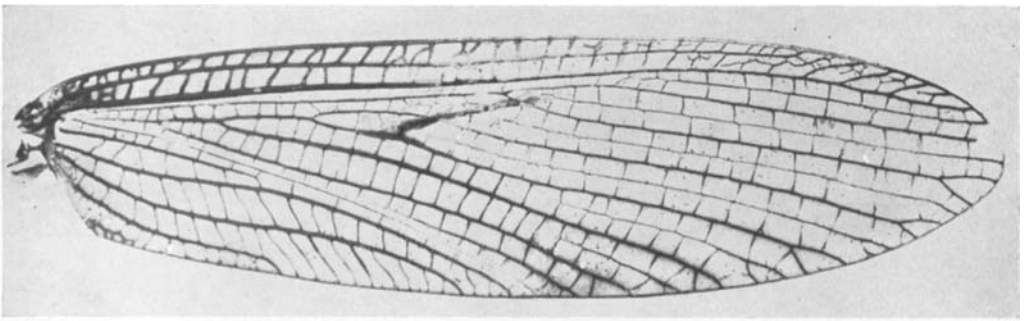
Venation pattern found in *Chaeteessa* is the most primitive amongst mantids.

Venation of *Chaeteessa* is complete and blattid in its characteristics.

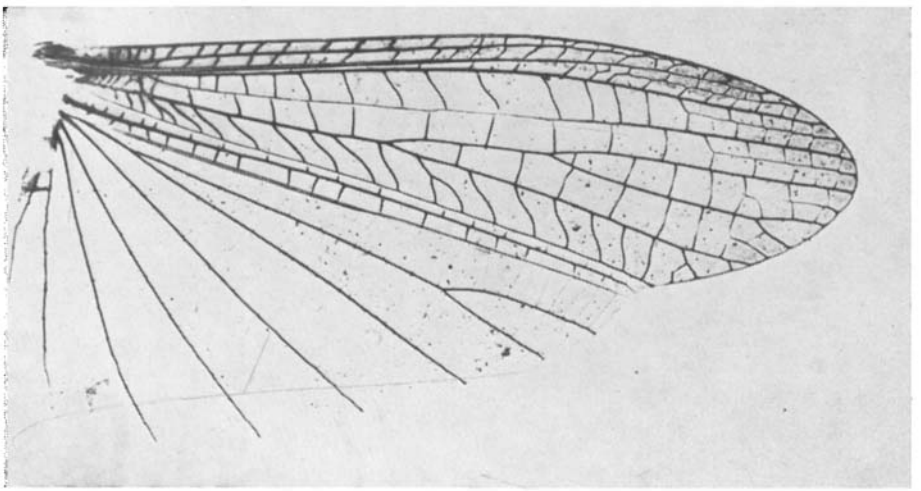
Wings of *Metallyticus* show a great reduction in the development in the hind-wing of vein 1V of *Chaeteessa* and *Periplaneta*. 1V is, however, definitely present, preceded by a recognisable Pcu and followed by a branching 2V.



1



2A



2B

Chaeteessa filata Burm.

1. Fore-leg. 2A. Fore-wing. 2B. Hind-wing.

Wings of other mantids have lost vein 1V in the hind-wing ; branching vannal vein immediately behind Pcu is homologous with branching 2V of *Chaeteessa* and blattids.

ACKNOWLEDGMENTS

I wish to thank Professor C. G. Varley for allowing me to examine a specimen of *Chaeteessa* (probably *C. filata* Burm.) and permitting me to mount and photograph a fore-leg and the wings (figs. 1 and 2 of the plate). I am also indebted to Dr. D. R. Ragge who allowed me to examine specimens of *Chaeteessa*, *Metallyticus* and other genera in the Department of Entomology, British Museum (Natural History), and for the identifications of the wings in text-figs. 3 and 4. No specimens of *Chaeteessa* and *Metallyticus* were available in the Museum of Zoology, Cambridge.

SUMMARY

The wings of *Chaeteessa* are described and the condition of venation commented on. Venation is primitive and blattid-like.

Features of the wings of *Metallyticus* are described briefly.

Comments are made on venation in other genera of mantids and a remarkable uniformity of venation noted. The way in which venation in these other mantids differ from that of *Chaeteessa* and *Metallyticus* is considered and homologies are determined.

The unique primitiveness of *Chaeteessa* is confirmed.

REFERENCES

CHOPARD, L. (1943). Orthoptêroïdes de l'Afrique du Nord. *Faune de l'Empire Francais* **1**, 1–450. Paris : Larose.

CHOPARD, L. (1949). Ordre des Dictyoptères. In Grassé's *Traite de Zoologie* **9**, 353–407. Paris : Masson.

GIGLIO-TOS, E. (1927). Orthoptera : Mantidae. *Das Tierreich*, Lief. **50**. Berlin & Leipzig : de Gruyter.

HANDLIRSCH, A. (c. 1930). Mantodea oder Fangheuschrecken. *in Kükenthal & Krumbach Handbuch der Zoologie*, **4**, i, 803–819. Berlin & Leipzig : de Gruyter.

LAMEERE, A. (1922). Sur la nervation alaire des insectes. *Bull. Classe Sci. Acad. roy. Belge.* (5) **8**, 138–149.

RAGGE, D. R. (1955). *The wing-venation of the Orthoptera Saltatoria with notes on the Dictyopteran wing-venation.* London : British Museum (Nat. Hist.).

SMART, J. (1952). The wing-venation of the American cockroach, *Periplaneta americana* Linn. (Insecta : Blattidae). *Proc. zool. Soc. Lond.* **121**, 501–509.

SMART, J. (1953 a). On the wing-venation of *Physemacris variolosa* (Linn.) (Insecta : Pneumoridae). *Proc. zool. Soc. Lond.* **123**, 199–202.

SMART, J. (1953 b). A note on the wing-venation of *Dissosteira carolina* (Linn.) (Insecta : Acridiidae). *Proc. zool. Soc. Lond.* **123**, 203–205.

SMART, J. (1953 a). The wing-venation of the migratory locust (*Locusta migratoria* Linn.) (Insecta : Acridiidae). *Proc. zool. Soc. Lond.* **123**, 207–217.

SMART, J. (in press). A note on insect wing veins and their tracheae. *Quart. J. micr. Sci.*

SNODGRASS, R. E. (1935). *Principles of insect morphology.* New York and London : McGraw-Hill.