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Wings of Male Scale Insects (Coccoidea)

Abstract - The shape and venation of the metathoracic wings of 94 male scale insects were evaluated. The shape is variable within family and generic levels ranging from elongate and narrow to broadly rounded and wide. The number of veins is reduced consisting of the radial and medial veins in advance taxa, while primitive taxa often have two additional creases representing the position of veins. The two veins in most taxa join at an acute angle in the basal area forming a basal stem that often extends to the margin. A notable feature is the greater length of this central basal stem from the primitive to advanced taxa.

Key words: Coccoidea, wings, scale insects, males.

INTRODUCTION

Flight in insects is projected to aid in the ability to disperse and occupy a variety of habitats, as well as contribute to species diversification resulting in flying insects representing over two-thirds of all species known. Capabilities include using wings to take advantage of the wind to sail from one location to another to take advantage of new food sources, finding mates, and escaping predators and parasitoids. Sailing performance is projected to have improved steadily with increased wing size, with even the smallest wings significantly increasing sailing velocity compared to wingless specimens. Two general hypotheses dominate regarding the origin of insect wings. The first assumes the wings evolved by modification of limb branches that were already present in theoretical multibranching ancestral appendages perceived to function as gills (Kukalova-Peck, 1987). This basic hypothesis purports insect wings evolved from articulated gill plates of aquatic ancestors through an intermediate semi-aquatic stage. The second projects that wings arose as outgrowths (paranotal processes) of the body wall, not directly related to any pre-existing limbs (Hinton, 1977). The next advancement proposed is the development of a wing-flexion mechanism in the Upper Carboniferous era (Carpenter, 1977). He believed this provided radiation capability and protection from natural enemies. Pedley (1995) reported that lift could also be enhanced by circulation created during pronation and supination by rotational

mechanisms. However, a significant disparity in fossil records obscures the origins of wings, and hence flight. Flight and development are the two primary factors considered in the separation of the phylogenetic lines for higher taxa in taxonomic schemes (Carpenter, 1953).

The presence of one pair of wings on the metathorax in males has generated a great degree of speculation regarding the appearance of possible primitive ancestors. Both Borchsenius (1956) and Kawecki (1964) projected that both male and female possessed two pair of wings. Kawecki proposed that the hamulohalter functioned as a frenulum with a number of bristles to connect the two wings, which were gradually lost in the female over time. With no intermediate form available from the fossil records, speculative conclusions on potential ancestors do not conform to known fossil records. It is interesting to note that over 240 fossil records for males have been discovered from the Upper Triassic to the Upper Miocene deposits (Koteja 1989) with wing patterns similar to modern taxa perceived to be primitive (*Matsucoccus larssoni* Koteja) and advanced (*Kuenowicoccus pietrzeniukae* Koteja). Koteja (1989) noted that these fossil specimens, consisting of both males and females, represent all major family groups. The scale insects are projected to have been present as early as the Permian Era (Borchsenius 1958), while Hoy (1962) and Danzig (1980) suggested they emerged in the Cretaceous Era simultaneously with the angiosperms. However, Koteja (1989) conclude from paleontological data that the major families were present in the Eocene and some species had acquired a high degree of specialization by the Upper Cretaceous.

A diversity of wing features occurs in species within the 22 to 27 family level taxa. Ghauri (1962) provided detailed illustrations and descriptions for the wings of 24 species of Diaspididae. Several investigators have included wing descriptions for specific species within their studies (i.e., Miller & Denno, 1977; Miller & Lambdin, 1978; Miller et. al., 1984; Ray & Williams, 1983). The goal of this study was to determine and compare the wing features between male Coccoidea. The various degrees of wing development may be useful in delineating affinities among species groups.

MATERIALS AND METHODS

We processed and analyzed the males of 94 species. Data on the wings were obtained by viewing and measuring the structures with a Wild microscope. Photographs of the wings for the species were taken with an Olympus stereoscope equipped with a camera with images processed using Adobe Photoshop®. Data recorded on wing features in the taxa studied included: the number and location of veins, length and width of wings, density of veins, wing shape and area.

RESULTS

The most prominent features of the wings are the shape and vein structure. The shape and size of the membranous pair of wings on the metathorax are variable within

the family, but potentially provide sufficient ancillary characters to aid in determining affinities within the Coccoidea. The basal area of the wing usually has an alar lobe often with an invaginated pocket for receiving the bristle(s) of the hamulohalter. However, the hamulohalter or bristles are lacking in many species. Wing size is similar among members within a given population; however, members of some species may exhibit either a macropterous or brachypterous condition (eg., *Quadraspidiotus* spp.), while other species are apterous (eg., *Comstockiella sabalis*). The surface of the wing is covered with numerous microtrichia and appears wave-like to a degree in most specimens, while several species with minute or atrophied veins often have fewer microtrichia and appear smooth. Wing shape within the primitive taxa range from: (a) broad based elongated wing blade with broadly rounded apical margin; (b) with an acute apical margin; (c) a fully extended leather-like costal margin; (d) costal and anal margins parallel; or (e) with a straight costal margin and a broadly rounded apical margin that merges gradually with the anal margin, the latter merging with an elaborate lobe-like anal area. Also, the wing surface may be sculptured, with corrugated or pinnate folds, or pigmented. In the advanced taxa, wings are elongated or globular with: (a) rounded apical margin; (b) an acute apical margin; (c) costal and anal margins parallel; (d) costal margin straight and the anal margin rounded; or (e) an elongated wing with a narrow base. A few species exhibit pigmentation, especially in the costal area (e.g., *Circulaspis* sp.).

The general vein formation observable in wings of existing primitive species (Fig. 1) consists of: (a) costal complex: (costa + sub-costa), (b) radius, (c) radial sector, (d)

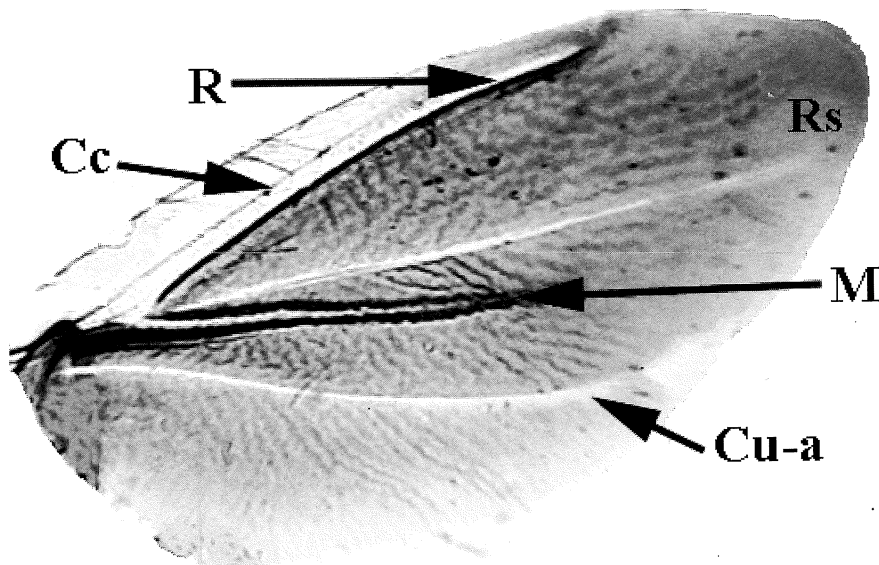


Fig. 1 - General wing type in primitive male scale insects: cc = Costal complex, Cu-a = Cubito-anal crease, M = Medial vein, R = Radial vein, Rs = Radial sector.

medial, and (e) cubitus (represented by a crease or cubito-anal vein). Venation is rudimentary with two visible veins, the radial and medial (Patch, 1909). In most instances, the longitudinal vein system arises at one point within the wing base as a basal stem. The veins remain undivided for a short distance and then diverge into two veins at an acute angle. These veins may be equal or unequal in length, curved or straight, thick or thin, depending on the species. In species representing several genera, the radial and medial veins remain separated in the basal area. These longitudinal veins contribute to strengthening the wing. In several species, a thick basal stem is prominent in the basal area with the diverging veins becoming smaller and less rigid distally. In more primitive taxa, creases or channels are present running parallel to the longitudinal veins in several species. These appear concave and extend variable distances depending on the species.

These creases representing vein positions may occur between the costal margin and radial vein, between the radial and medial veins, and occasionally posterior to the medial vein. The distinctive vein patterns discernible in the more primitive species evaluated are: (a) all vein positions visible and originating from the base to form a basal stem that becomes bifurcated ca. 1/5th the distance into the wing, veins equal in length with at least one (usually the cu-a) crease arising independent of the veins (e.g., *Aspidoproctus* sp., *Crypticerya* sp., *Drosicha* sp.); (b) vein pattern similar except the medial vein is reduced (or faint) and veins are unequal in length (e.g., *Calipappus* sp., *Coelostomidia* sp., *Drosicha* sp., *Monophlebidus* sp., *Ultracoelostomidia* sp.); and (c) veins similar to latter except basal stem does not extend into the basal plate (e.g., *Llavea* sp.).

With the exception of the radial and medial veins, which form a fork, all other veins or evidence of veins are lost or fused in the advanced taxa (Fig. 2). The dominant vein

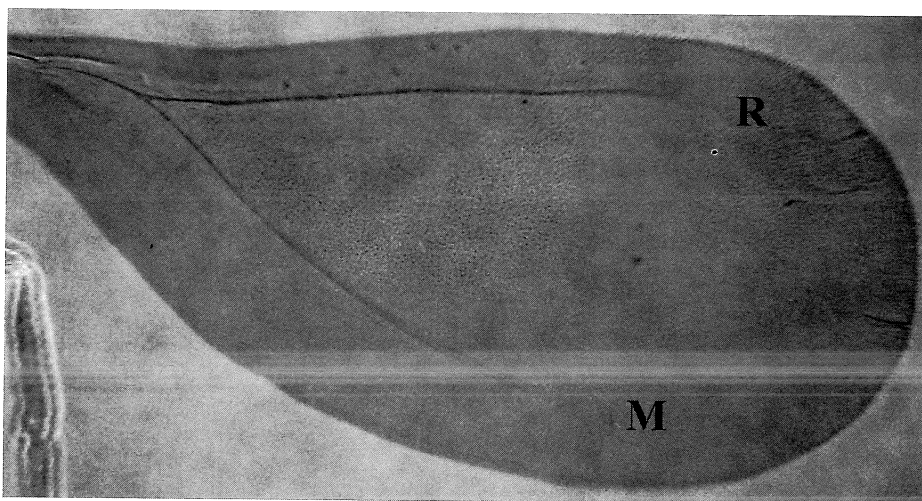


Fig. 2 - General wing type in advanced male scale insects: M = Medial vein, R = Radial vein, Rs = Radial sector.

patterns in the more advanced males are: (a) basal stem long (extending ca. $1/5^{\text{th}}$ to $1/4^{\text{th}}$ the distance into wing), veins arising at wing base with radial and media veins joined to basal stem, and veins unequal in length with at least the radial vein extending into subapical area (e.g., *Aspidiotus* sp., *Chionaspis* sp., *Diaspidiotus* sp., *Chrysomphalus* sp., and *Quadraspidiotus* sp.); (b) basal stem long, with veins joined and equal in length, but veins reduced in length extending about $1/2$ to $2/3^{\text{rd}}$ the length of the wing (e.g., *Abgrallaspis* sp., *Aonidia* sp., *Aspidiella* sp.); (c) basal stem short (extending ca. $1/6^{\text{th}}$ the distance into wing), veins joined but unequal in length, with at least radial vein extending into subapical area (e.g., *Dactylopius* sp., *Cerococcus* sp.); (d) basal stem short, arising at base with veins joined and equal in length (e.g., *Diaspis* sp.); (e) radial vein arising within basal area with no common basal stem, veins separated and unequal in length (e.g., *Allokermes* sp., *Dactylopius* sp., *Hypogeococcus* sp., *Lecanodiaspis* sp., *Leucaspis* sp., *Phenacoccus* sp., *Planococcus* sp., *Rhizaspidotus* sp.); (f) radial vein arising within basal area with no common basal stem, veins separated and equal in length, (e.g., *Eriococcus* sp.); (g) basal stem absent, veins separated and arising a short distance from margin in basal area, veins equal in length (e.g., *Aclerda* sp., *Toumeyella* sp.). In some species of Pseudococcidae, Kermesiidae, and Diaspididae, the base of medial vein is disjointed from the radial vein leaving a small gap in the basal area before its demarcation into the wing. In other species, the veins are unequal in length with the medial vein faint or lacking. (e.g., *Allokermes* sp.). In wings where the medial vein does not join with the radial vein, the size of the gap often varies among the species.

CONCLUSIONS

A narrow wing base, shorter veins, globular hamulohalter, and the gradual petiolation occurring in various species, even within the same family level taxa, may represent apomorphic features. The primitive species have two dominant veins (radial and medial) and remnants or creases representing vein positions. With the exception of these two veins that emerge from a basal stem, all other veins are lost or fused in the advanced taxa. Most lecanoid and diaspidoid taxa retain the radio-medial fork. Kawecki (1964) concluded that the wings of Margarodidae and Lecaniidae were similar, but differ more from species of Diaspididae. He believed the reduction of the hamulohalter and accompanying bristles were evidence of advancement. The basal stem in the primitive wing is short and broad, while it is longer and more slender in the advanced species. The shape and venation of the wings often vary within the families. A similar vein pattern was observed in several genera (e.g., *Abgrallaspis* and *Quadraspidiotus*); however, the vein pattern may differ among species within the same genus. Although the appearance and number of veins are irregular within the Coccoidea, these features appear consistent for the species. Because of the small sample size (94 of over 7,000 species), no specific conclusions can be made for the male scales as a whole. It is anticipated that additional wing patterns will be discovered as more species are investigated.

REFERENCES

- BORCHSENIUS N. S., 1958 - On the evolution and phylogenetic relations of the Coccoidea (Insecta, Homoptera) - Zoologicheskii Zhurnal, 37: 765-780.
- CARPENTER F. M., 1953 - The geological history and evolution of insects - Amer. Scientists, 41: 256-270.
- DANZIG E., 1980 - Coccids of the Soviet Far East - Nauka. Leningrad, 367pp.
- GHAURI M. S., 1962 - The morphology and taxonomy of male scale-insects (Homoptera: Coccoidea) - Alard and Son, Bartholomew Press, Dorking, 221pp.
- HINTON H. E., 1977 - Enabling mechanisms - Proc XVth Intern'l. Cong. Entomol., 71-83.
- HOY J. M., 1962 - Eriococcidae (Homoptera: Coccoidea) of New Zealand - New Zealand Dept. Sci. and Industry Res. Bull., 146:1-219.
- KAWECKI Z., 1964 - The importance of the degree of reduction in male wing apparatus for studies on the phylogenesis of scale insect (Homoptera: Coccoidea) - Zool. Poloniae, 14: 205-214.
- KOTEJA J., 1989 - Paleontology. pp. 149-163. in Armoured scale insects, their biology, natural enemies and control. Rosen, D. (ed.), Vol. A. - Elsevier Sci. Publ., Amsterdam.
- KUKALOVA-PECK J., 1987 - New carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta) - Can. J. Zool., 65: 2327-2345.
- MILLER D.R., LAMBDIN P. L., 1978 - A new genus and two new species of asterolecaniid scale insects on palm from Colombia and Trinidad (Homoptera: Coccoidea: Asterolecaniidae) - Proc. Entomol. Soc. Wash., 80: 240-263.
- MILLER D. R., DENNO R. F., 1977 - A new genus and species of mealybug with a consideration of morphological convergence in three arboreal species (Homoptera: Pseudococcidae) - Systematic Entomol., 2:111-157.
- MILLER D. R., DAVIDSON J. A., STOETZEL M. B., 1984 - A taxonomic study of the armored scale *Pseudidnaspis Hempel* (Homoptera: Coccoidea: Diaspididae) - Proc. Entomol. Soc. Wash., 86: 94-109.
- PATCH, E., 1909 - Homologies of the wing veins of the Aphididae, Psyllidae, Aleurodidae and Coccidae - Ann. Entomol. Soc. Amer., 2:101-136.
- PEDLEY, T. J., 1995 - Biological-fluid-dynamics. pp.109-129. in Symposia of the Society for Experimental Biology - Ellington, C. P. (ed.), No. 49. Company of Biologists Ltd., Cambridge, UK.
- RAY, C. H., WILLIAMS, M. L., 1983 - Description of the immature stages and adult male of *Neolecanium cornuparvum* (Homoptera: Coccoidea) - Proc. Entomol. Soc. Wash., 85:161-173.