

# Wing Folding in the Hymenoptera

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**ABSTRACT** Longitudinal folding (plaiting) of forewings at rest has arisen independently in Vespidae, Colletidae, Gasteruptionidae, Figitidae, Leucospidae, and Pompilidae. In the first five families the plaiting fold is similar in position, but in the last family its position is different. A type of wing folding unique to the eucoilid genus *Kleidotoma*—wrapping flexure—is described. In all cases, evolution of wing folding is associated with modifications of wing morphology (most commonly, regions of vein flexibility termed alar fenestrae). The mechanism of wing folding in the family Vespidae includes a “click” mechanism at the intersection of the plaiting fold and the claval furrow in the region of vein cu-v; it has only two stable positions, inverted and everted, giving the vespid forewing only two stable configurations, fully unfolded and fully folded, respectively. Folding involves movement of the third axillary sclerite and vannal vein in addition to hind wing movements; unfolding is probably partly the result of vannal movement of the hind wing as the wasp prepares to fly but can occur even if a hind wing has been removed. Teneral *Polistes* wasps lack plaiting folds for about 36 h after eclosion. Removal of either a teneral hind wing or the hamuli of a teneral hind wing often permanently prevents folding of the ipsilateral forewing, indicating that the hind wing hamuli are important in fold development. Folding of vespid wings may help to protect them from damage in close quarters. Folding of colletid, leucospid, and pompilid wings may be mimetic of vespids, an idea supported by the fact that diverse groups of wasplike Hymenoptera, Diptera, and Lepidoptera have forewings with a darkly pigmented leading half that appears to enhance their resemblance to Vespidae. Folding in Figitinae and *Kleidotoma* may allow less hindered movement through moist dung and decaying plant and fungal material, the habitats of their fly hosts.

**KEY WORDS** Insecta, wing morphology, mimicry, Hymenoptera

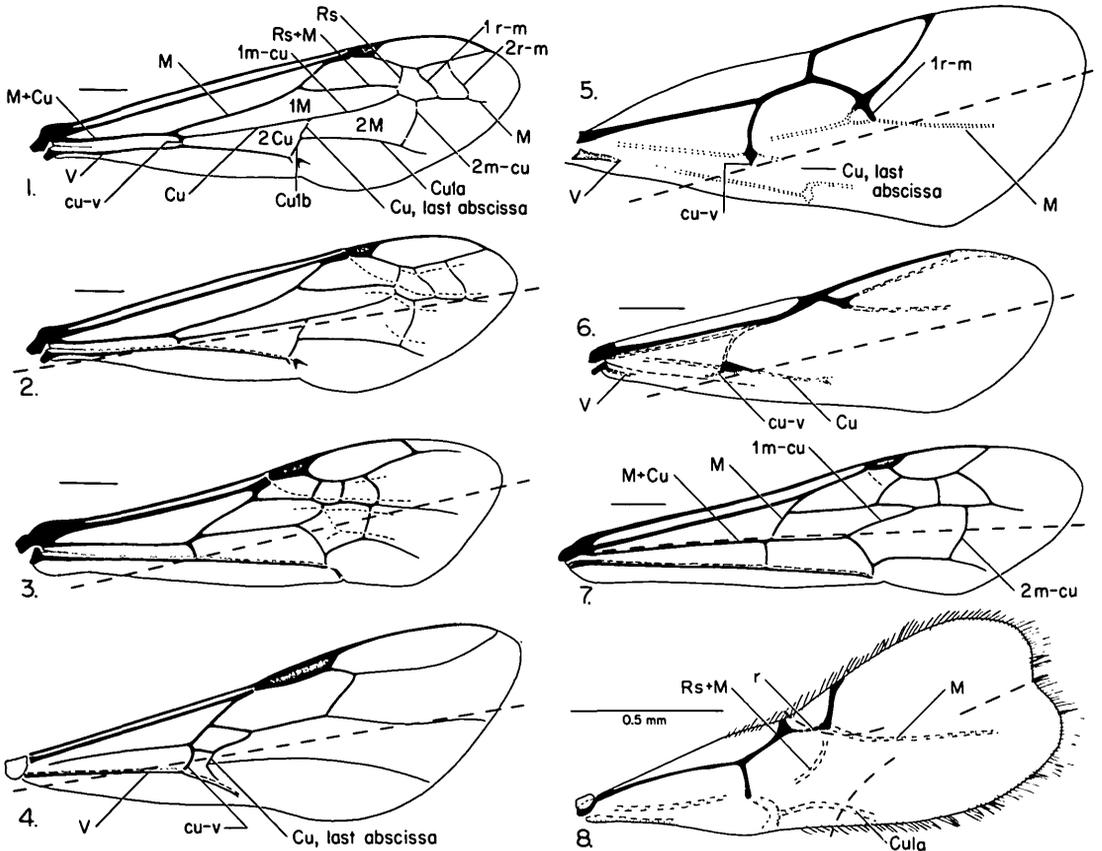
MOST ENTOMOLOGICAL textbooks indicate that longitudinal folding, or plaiting, of the forewings at rest is a unique character of the Vespidae (excluding the Stenogastrinae, Euparagiinae, and most Masarinae). However, similar folding occurs in other Hymenoptera: the Leucospidae (Bouček 1974), the Gasteruptionidae (Crosskey 1962), the subfamily Figitinae of the Figitidae (Weld 1952), and the closely related pompilid genera *Episyron* and *Poecilopompilus* (Evans 1950, 1951a,b, 1966). It has not been reported before that comparable folding is also found in bees of the colletid genus *Eulonchopria*.

Because these taxa are in separate superfamilies (Vespoidea, Chalcidoidea, Evanioidea, Cynipoidea, Pompiloidea, and Apoidea, respectively), the plaiting fold clearly evolved independently in each case. In fact, the plaiting fold may have arisen twice in the Vespidae and been lost in some members of this family, depending on the phylogenetic positions of the Euparagiinae, Masarinae, and Stenogastrinae. (See Carpenter [1982] for a recent phylogenetic study.) The phylogeny of the genera of Masarinae would also be important in investigating origins and losses of wing folding, which occurs in only two sections of that subfamily, the genus *Celonites* and the *Quartinia* group (Richards 1962). Some specimens of the chalcidoid genus

*Heimbra* suggest that wing plaiting similar to that in leucospids may also occur in this group, but with limited material available we cannot confirm this.

In addition, we consider a type of wing folding or bending described by Vet and Alphen (1985) for the eucoilid genus *Kleidotoma* (Cynipoidea: Eucoilidae). Such folding results from what we call wrapping flexures rather than plaiting folds.

The folds should not be confused with the wing flexion lines (terminology of Wootton [1979, 1981]), which are common features of insect wings. Wing flexion lines in the Hymenoptera (Fig. 2) are all concave above (Mason 1986) and include the following: The claval flexion line (vannal fold of Snodgrass [1935] and anal furrow of Duncan [1939]), which is parallel to and directly costad of the vannal vein (we follow Snodgrass [1935] in the use of the term vannal vein; in Hymenoptera it is the same as the so-called anal vein); the wing flexion lines located between the radial and medial veins (here referred to as the radial flexion lines); and those between the medial and cubital veins (here referred to as the medial flexion lines). Flexion lines, when present, are associated with alar fenestrae (localized pale or transversely striate regions of veins) where the lines cross veins (see Wootton 1981). The alar fenestrae most commonly seen in hymenopteran forewings (Fig. 1 and 2) are



**Fig. 1-8.** Forewings, showing plaiting folds (heavy dashed lines) and wing flexion lines (weak dashed lines). Scale lines represent 1 mm except for Fig. 8. (1) Vespidae, *Vespula maculifrons*, with cells and veins labeled. (2) Vespidae, *Vespula maculifrons*. (3) Colletidae, *Eulonchopria punctatissima*. (4) Gasteruptiidae, Hyptiogastrinae (based on Crosskey [1962]). (5) Figitidae, Figitinae, *Melanips* sp. (based on Nordlander [1984]). (6) Leucospidae, *Leucospis affinis* Say. (7) Pompilidae, Pompilinae, *Poecilopompilus* sp. (8) Eucilidae, *Kleidotoma* sp. Wing illustrations use the conventions of Mason (1986)—spectral veins shown by dotted lines, nebulous veins shown by dashed lines and light stippling, and tubular veins shown in solid black.

those located on the second free abscissa of Rs (called simply Rs below) and on the two r-m veins (associated with the radial flexion lines), the two m-cu cross veins (associated with the medial flexion lines), and vein cu-v and the end of vein Culb (associated with the claval flexion line). The wing flexion lines and corresponding alar fenestrae are thought to be responsible for the complex wing shape changes occurring in flight (Wootton 1981; Ellington 1984, 69-70; Mason 1986).

**Materials and Methods**

Observations on fold positions and wing morphology in wing-folding groups and related taxa were based on pinned museum specimens. The mechanism and development of the plaiting fold in the Vespidae was studied in living and freshly killed wasps. Casual field observations of *Eulonchopria* were made by C.D.M. at the Chamela field station of the Universidad Nacional Autonoma de Mexico.

Vespid wasps were collected in the vicinity of Lawrence, Kans. Mature wasps were caught on their nests or visiting flowers. Teneral wasps were obtained by cutting the silk caps off closed cocoons and thereafter keeping the nests in plastic boxes. Nests were checked repeatedly throughout the day for recently eclosed adults within cocoons or on the floor of the box. Removal of the silk caps allowed early detection of eclosion. Wasps were individually marked on the mesoscutum using a Rapidograph pen and Liquid Paper (Liquid Paper, Boston, Mass.).

Prior to all manipulations, wasps were cooled in a refrigerator. In all of the experiments only the wings on one side were manipulated; the opposite side was used as a control. In the hind wing-removal experiments, the wing was cut at its base. Hamuli were removed by peeling off a strip along the costal margin of the hind wing.

Most behavioral observations were made in a 1-m<sup>3</sup> flight cage. For stroboscopic observations wasps were tethered with wire or dental floss attached by

wax to the mesoscutum (technique of Hollick [1940]). A Winsco E-43 stroboscope (Wabash Instrument Corporation, Wabash, Ind.) was used, and its flash frequency was adjusted until the wings appeared nearly stationary.

### Observations and Results

**The Plaiting Folds.** Plaiting folds in all six taxa are convex above—that is, the ventral wing surfaces are brought together in folding—and the folds are relatively straight. Two fold locations are distinguishable; plaiting fold A, shown by the Vespidae, *Eulonchopria*, Gasteruptiidae, Figitinae, and Leucospidae (Fig. 2–6); and plaiting fold B, shown by the pompilids *Episyron* and *Poecilopompilus* (Fig. 7).

Plaiting fold A, as illustrated by the Vespidae (Fig. 2), starts on the posterior margin of the wing near the wing base and extends obliquely across the vannal vein proximal to vein cu-v. It passes through the alar fenestra of vein cu-v and continues diagonally across the second cubital cell, the last abscissa of vein Cu, the second medial cell, and vein 2 m-cu at the anterior of the two alar fenestrae of this cross vein. Finally, the fold extends obliquely across the distal extension of the medial vein toward the wing tip. The wing is folded acutely along most of its length, becoming only slightly less acute at the base (between vein cu-v and the vannal margin of the wing) and at the tip (beyond vein 2 m-cu). In vespids in which wing plaiting occurs, an alar fenestra is present on the last abscissa of Cu; it is lacking in those vespids that do not plait their wings. This is the only modification of the vein pattern found to be associated with the plaiting fold in the Vespidae.

Because of the similarity between the wing vein patterns of the Vespidae and *Eulonchopria* (Fig. 3), it is clear that the plaiting fold lies in a similar position with respect to the wing venation in both taxa. Therefore *Eulonchopria* is considered to have plaiting fold A. *Eulonchopria*, unlike the Vespidae, has no alar fenestra on the last abscissa of Cu, and the plaiting fold does not pass through an alar fenestra on vein 2 m-cu. Instead, the fold passes through the midpoint of that vein between the two fenestrae. No localized weakening can be seen at this point; the vein merely bends. These differences are most likely because the wing is less acutely folded in *Eulonchopria* than in vespids.

Although the Gasteruptiidae (Fig. 4) have a vein pattern quite distinct from those of Apoidea and Vespidae (extremely reduced second cubital cell, 2 m-cu cross vein absent), the position of the fold relative to the wing venation is of type A. The Gasteruptiidae show a weakening of the last abscissa of Cu (at the point at which the plaiting fold crosses the vein, as in the Vespidae) and of cu-v along much of its length. Interestingly, the fold does not pass through the fenestra in this vein. These regions of weakening are too diffuse to be termed fenestrae but are clearly associated with

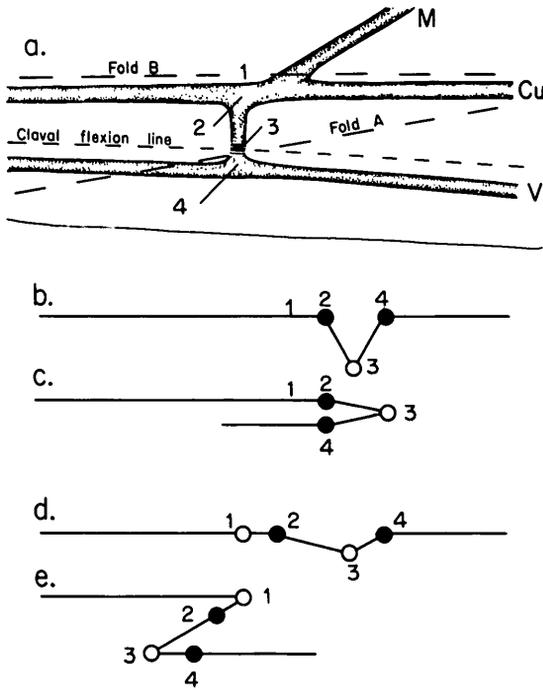
the fold because in the related nonplaiting families Aulacidae and Evaniidae, neither weakening is apparent. In gasteruptiids the fold is uniformly acute along its length except that it becomes less acute at either end, as in the Vespidae.

The figitine wing venation (Fig. 5) has still fewer elements, yet the fold passes across the vannal vein, the faint vein cu-v, the last abscissa of Cu, and the distal extension of M as in the aforementioned groups. The figitine fold appears to be the most acute of all the groups here described, probably because of the lack of sclerotized (tubular, to use the terminology of Mason [1986]) veins across the path of the fold.

In the Leucospidae (Fig. 6), because of the highly reduced wing venation, it is difficult to establish the exact path of the fold relative to the veins. Because it begins on the hind margin of the wing, away from the wing base, and appears to pass through the vicinity of cu-v and to cross Cu, we consider it plaiting fold A. As in the other groups, the plaiting fold is acute along the majority of its length, becoming weaker near the wing margins.

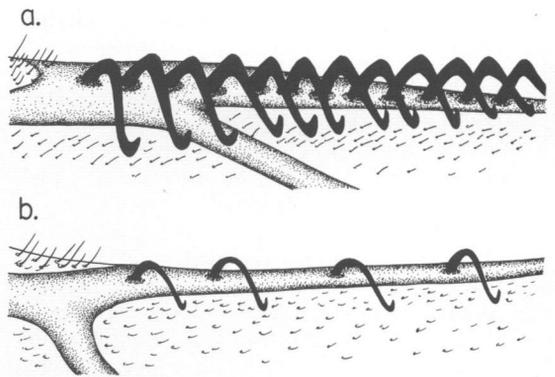
In the pompilid genera *Episyron* and *Poecilopompilus* the fold lies in a completely different position with respect to the wing venation and will be termed plaiting fold B (Fig. 7). In these genera the fold originates at the wing base immediately costad of vein M+Cu and extends distally closely parallel to M+Cu. It passes through the basal vein (M) at a distinct alar fenestra not found in the groups listed above and continues parallel to vein Cu to the junction of Cu and 1 m-cu. After passing through 1 m-cu at a region of slight vein weakening, it crosses the second medial cell and finally 2 m-cu. Plaiting fold B is very weak at the wing base. It is increasingly acute up to the point at which it crosses the basal vein and is thereafter gradually weaker, becoming distally a gradual curvature of the entire 2 m-cu cross vein.

Fig. 9a shows diagrammatically the different positions of plaiting folds A and B in the vicinity of vein cu-v. Because plaiting fold B runs parallel to, and separate from, the claval flexion line for its entire length, the two folds, one convex and the other concave, allow the whole wing to assume a Z-shape in cross section when folded (Fig. 9d and e), which is not possible in those wings with plaiting fold A (Fig. 9b and c). Although our discussion of plaiting fold B has focused entirely on two pompilid genera, a homologous fold and fenestra in vein M are present in almost all genera of Pompilinae, although the fold is less acute, and therefore less conspicuous, and the fenestra less localized. Other pompiline genera that show this fold quite distinctly are *Anoplius*, *Aporinellus*, *Paracyphonyx*, and *Aplochaes* (Evans 1950, 1951a,b, 1966), and it is possible to find museum specimens of each of these genera with the forewing in a folded position; however, in none of them is the fold as fully developed as in *Poecilopompilus* and *Episyron*.



**Fig. 9.** (a) Diagram of region of vein cu-v in wasp or bee forewing showing plaiting folds A and B and claval flexion line (both folds do not occur in any one species). 1, point through which fold B passes in radial cell; 2, intersection of veins M+Cu and cu-v; 3, fenestra in vein cu-v; 4, intersection of veins V and cu-v. (b and c) Diagrammatic cross section of vespid wing through points 1, 2, 3, 4 in unfolded and folded positions of plaiting fold A. Black circles represent veins; open circles represent folds. (d and e) Diagrammatic cross section of *Pocillopompilus* wing through points 1, 2, 3, 4 in unfolded and folded positions of plaiting fold B. Black circles represent veins; open circles represent folds.

**The Wrapping Flexures.** The eucoilid genus *Kleidotoma* (Fig. 8) shows a peculiar type of wing bending which allows the wings to be wrapped over the dorsum of the metasoma (Vet & Alphen 1985). In contrast to the folds described above, the flexures in *Kleidotoma* wings are neither primarily longitudinal nor acute. In the flexed position, the distal two-thirds of the two forewings are precisely overlapping, and the hind wings are beneath them. The distal half of each forewing is nearly symmetrical around a longitudinal median axis that ends in an apical notch. On either side of the apical notch the overlapping surfaces are flexed downward, making a weak, dorsally convex median longitudinal fold in each forewing. Two other convex folds, one extending from the costal margin and one from the vannal margin, allow the distal half of the wing to be flexed downward toward the surface of the metasoma. When the wings are overlapped, the fold on the costal margin of one forewing corresponds precisely to the fold on the vannal margin of the other, so that the two forewings fold around the metasoma. Modifications of the



**Fig. 10.** Costal margin of hind wing of *Vespula maculifrons* (a) and *Eulonchopria punctatissima* (b) showing hamuli.

wing associated with folding include weak sclerotization of vein r, a weak notch on the costal margin that improves the symmetry of the apical half of the wing, and of course the notch at the wing apex.

**Mechanisms of Wing Folding and Unfolding in Vespidae.** Because plaiting fold A does not extend to the axillary triangle (the region of the wing attached to the body and containing the axillary sclerites), we initially presumed that folding occurs as a result of forces extrinsic to the forewing base. In *Polistes* wasps in a flight cage, both plaiting of the forewing upon landing and unfolding prior to flight appear to result from movements of the ipsilateral hind wing attached to the hind edge of the forewing by hamuli. Coupling of the wings by hamuli (Fig. 10) makes all Hymenoptera functionally two-winged in flight. Movement of the hind wing costad relative to the forewing would fold the posterior region of the forewing beneath the anterior region. Movement of the hind wing in the reverse direction would unfold the forewing.

However, removal of a hind wing from mature vespid wasps—Eumeninae: *Monobia quadridens* (L.) ( $n = 1$ ), *Odynerus* sp. ( $n = 1$ ); Polistinae: *Polistes metricus* Say ( $n = 7$ ), *P. fuscatus* (F.) ( $n = 5$ ), *P. exclamans* Viereck ( $n = 7$ ), *P. annularis* (L.) ( $n = 2$ ); Vespinae: *Vespula maculifrons* (Buysson) ( $n = 6$ )—did not eliminate folding of the ipsilateral forewing. Wasps take slightly longer (2–10 s) after landing to fold the forewing on the manipulated side than on the control side—Polistinae: *P. annularis* ( $n = 56$ ), *P. metricus* ( $n = 195$ ), *P. exclamans* ( $n = 147$ ); Vespinae: *V. maculifrons* ( $n = 94$ ) ( $n =$  number of landings observed;  $\chi^2 = 36.69$ ,  $P < 0.001$ )—and the forewing on the manipulated side trembles prior to folding in a way that is not seen in control wings. In addition, forewings removed from freshly killed wasps remain folded. Clearly the wings themselves have a natural tendency to fold up. Given this tendency, presumably resulting from the ultrastructural configuration of the cuticle along the plaiting fold, a more appropriate question is, what causes the wing to remain unfolded for short intervals after landing and, more

importantly, what prevents the wing from folding up in flight? The answer lies in a simple "click" mechanism in the forewing, which results in the wing having only two stable positions: completely unfolded or completely folded.

The click mechanism is located where the claval and plaiting folds cross—i.e., at the point at which they pass through vein cu-v. In the unfolded position, the claval fold at this point is acutely concave dorsally such that the alar fenestra of cu-v is well below the plane of the wing (Fig. 9b) and vein cu-v is partly hidden in dorsal view; we speak of the click mechanism in this position as inverted. When the wing is folded, the deep concavity along the claval fold disappears and the wing becomes strongly convex along the plaiting fold (Fig. 9c); the click mechanism is everted. In freshly killed specimens one can easily fold and unfold the forewing by gently grasping vein cu-v with forceps and inverting the folds as they pass through this position. Once in one of the two stable positions, folded or unfolded, it is difficult to cause the wing to move to the other without changing the configuration of vein cu-v.

In living wasps, transition from one stable position to the other appears to be accomplished by a combination of factors. Although the wing has a natural tendency to fold, if the click mechanism is inverted (the wing is in the fully unfolded position) folding is opposed. Therefore, eversion of the click mechanism must occur for folding to take place. Observations of large, slow-moving *P. annularis* that lacked hind wings indicated that plaiting occurs only when the wing is brought back along the long axis of the body, called wing flexion by Snodgrass (1935) and others. Furthermore, in freshly killed wasps, the click mechanism can be everted by applying pressure to the costal margin of the wing such that the wing is slowly flexed back along the body. The click mechanism is gradually everted until the wing snaps into the folded position (eversion occurs when the long axis of the wing reaches an angle of 40–60° to the body axis).

In neopterous insects, wing movements of this sort are caused by the contraction of muscles inserting on the third axillary sclerite, whose forces are transmitted to the vannal vein (Snodgrass 1935, 231). Fig. 11 shows the configuration of these sclerites and veins in the wing of a vespid wasp. In freshly killed vespids, as the forewing is flexed toward the long axis of the body, the distal end of the third axillary sclerite rotates upward out of the plane of the wing and toward the midline of the body. As a result of the rotation of the third axillary sclerite, the vannal sclerite, which is the proximal end of the vannal vein, moves toward the midline of the body passing *beneath* the posterior margin of the median plate (median axillary sclerite of Michener [1944]). The expanded vannal sclerite has a distinct protuberance on the dorsal surface nearest the trailing edge of the wing (Fig. 11), and as the protuberance slides beneath the median plate,

the vannal vein twists posteriorly (toward the trailing edge of the wing) along its long axis. In addition, the humeral plate (costal sclerite of Michener [1944]) tips down anteriorly. This combination of forces twists veins M+Cu and V in opposite directions, thus reducing the deep concavity in the claval flexion line which is between them, so that wing plaiting can occur. It is noteworthy that for *Vespula pennsylvanica* (Saussure) (Vespinæ), Duncan (1939) described three muscles inserting directly on the third axillary sclerite and one muscle which impinges on the third axillary sclerite by way of the subalare (a small ligament connects the subalare and the third axillary sclerite).

The importance of the vannal vein, third axillary sclerite, and associated muscles to the function of the click mechanism is further supported by the observation that it is possible to inactivate the click mechanism of mature wasps by cutting the tendinous connection between the third axillary sclerite and the vannal vein of the forewing. In both freshly killed ( $n = 5$ ) and living ( $n = 6$ ) *P. metricus* so treated, the manipulated wing remains completely folded, incapable of assuming the fully unfolded position. Close examination of these wasps shows that when the manipulated wing is forced to unfold, no deep concavity appears in the region of vein cu-v.

It is likely that the hind wing plays a supplementary role in normal wing folding because wasps with intact ipsilateral hind wings fold their forewings more rapidly than those lacking ipsilateral hind wings (see above). Occasionally, folding of unmanipulated forewings by wasps that lack ipsilateral hind wings seemed to occur as a result of normal metasomal grooming movements. Clearly a number of factors may contribute to eversion of the click mechanism and wing plaiting.

Wing unfolding requires that the click mechanism be inverted. As with eversion of the click mechanism, inversion seems related to the position of the wing relative to the body axis. In freshly killed wasps, the click mechanism can be inverted only when the wing is roughly at a right angle to the body. Furthermore, occasionally wasps preparing for flight appeared to unfold the wing simply by moving it costad. The hind wings may play a supplementary role in unfolding the forewings through their attachment to the posterior margins of the forewings by hamuli.

The most important function of the click mechanism is to maintain the wing in a fully unfolded position in flight. Stroboscopic observations of tethered *P. metricus* ( $n = 5$ ) in flight show that throughout the stroke cycle the wing remains fully unfolded. However, wings in which the click mechanism is destroyed by cutting the connection between the third axillary sclerite and vannal vein show moderate to complete folding along the plaiting fold during the stroke cycle (*P. metricus*;  $n = 9$ ). The most acute folding occurs at the top and the bottom of the wing stroke—at pronation

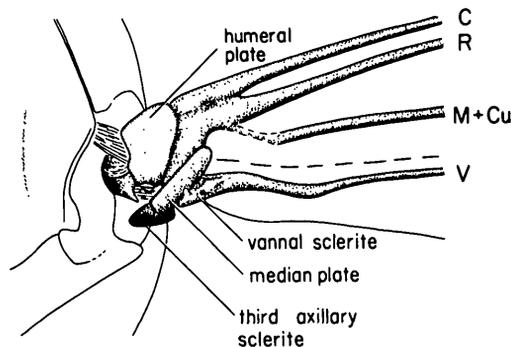
and supination—although even at intermediate points in the wing cycle, in comparison with the control wing, the experimental wing showed curvature along the plaiting fold. Plaiting becomes more acute at lower wing beat frequencies (as wasps fatigued).

**Mechanisms of Wing Folding in Other Taxa.** It was impossible to look in detail at the mechanism of wing plaiting in any of the other groups. However, series of pinned specimens of *Eulonchopria*, Leucospidae, Gasteruptiidae, and Figitinae suggest hypotheses on how wing plaiting occurs in these groups. The configuration of the wing at vein cu-v in Gasteruptiidae, Leucospidae, and Figitinae does not suggest a click mechanism. However, in unfolded *Eulonchopria* wings, the fold is most acutely concave at the cu-v cross vein, leaving the possibility that a click mechanism is involved in this genus. In pinned specimens of *Eulonchopria*, leucospids, and gasteruptiids, the frequently observed tight attachment of hind wings to the vannal edge of folded forewings suggests that when the two wings are attached by hamuli, movement of the hind wing costad beneath the forewing may be the proximate cause of wing folding. In none of the figitine specimens with folded wings were the hind wings attached to the forewings by the hamuli, suggesting that their mechanism of wing folding may be independent of hind wing movements.

Because plaiting fold B extends to the axillary triangle, it is possible that movements of the axillary sclerites could be responsible for plaiting. Costad movement of the vannal vein could cause the wing to assume the folded position. However, because in pinned specimens the plaiting fold is weak at the wing base, becoming most acute at about one-third the wing length, it is unlikely that initiation of wing plaiting occurs at the wing base. There is no morphological suggestion of a click mechanism as in the Vespidae. In addition, in plaited wings of *Poecilopompilus* and *Epsyron* specimens, one rarely sees the hind wings tightly hooked to the forewings as is common in vespids, *Eulonchopria*, leucospids, and gasteruptiids; a mechanism other than wing coupling is therefore likely.

Vet & Alphen (1985) report that wing flexion in *Kleidotoma* results from “stroking of the wings with their hind legs . . . and is significantly more prominent when kairomones [of their fly hosts] are present in the substrate [decaying plants and mushrooms].”

**Development of Wing Folding in Vespidae.** Because vespid adults have unfolded wings upon emergence from the pupa, one wonders when and how the plaiting fold appears in development of the wing. At 21°C, the wings of *P. metricus* are folded approximately 36 h after emergence from the pupal exoskeleton. In intact wasps each forewing is found to be folded only after the hamuli of the corresponding hind wing become attached to the forewing (*P. metricus*; *n* = 10). If a hind wing is removed from a teneral (1–10 h after eclo-



**Fig. 11.** Base of laterally extended forewing of *Polistes metricus* (tegula removed) showing exposed protuberance on vannal sclerite. Broken line represents the claval flexion line.

sion) adult *Polistes* (*P. metricus* [*n* = 20] and *P. fuscatus* [*n* = 5]), the corresponding forewing fails to become folded in 65% of the individuals. Control wings were folded in all but one of the *P. metricus*. In addition, if the hamuli are removed from one wing of a teneral adult, the ipsilateral forewing fails to develop the plaiting fold in 71% of the individuals (*P. metricus*; *n* = 14). In this experiment all control forewings were folded. These results indicate that the hind wing, through its attachment to the forewing by hamuli, plays a role in the ontogeny of the plaiting fold by folding the posterior part of the forewing beneath the anterior part during wing sclerotization. In those experimental forewings that failed to develop a plaiting fold, vein cu-v did not show the deep dorsal concavity seen in wings with a functioning click mechanism.

**Discussion**

For a fold to arise in a relatively rigid structure such as the hymenopteran forewing, regions of flexibility are necessary. The positions of the plaiting folds, wing flexion lines, and wing veins in six taxa indicate that repeated evolution of folding has occurred either through utilization of preexisting regions of vein flexibility (alar fenestrae) or through the evolution of novel regions of vein flexibility. The relative abundance of taxa with plaiting fold A, as opposed to plaiting fold B or the almost infinite number of potential fold positions, appears primarily because of the ubiquity and constancy in position of the alar fenestrae among the Hymenoptera (especially the fenestra on cu-v). That hymenopteran wings have a natural tendency to fold along the line represented by plaiting fold A is supported by the fact that it is not uncommon to find specimens of nonplaiting taxa with wings folded after removal from alcohol or other liquids.

We are uncertain as to the advantages, if any, of wing folding in Vespidae. Possibly, rather long unfolded wings are a hindrance or tend to be damaged in movements of the insect in narrow soil

burrows or cells like those of most Eumeninae. Presumably Eumeninae are ancestral in habits to other vespids; folding could have arisen in the protoeumenines and persisted in derived vespid groups that make other kinds of nests. For the Leucospidae and *Eulonchopria* we suggest that the folding is a matter of mimicry (see Bouček [1974, 15–16] for a discussion of mimicry in Leucospidae). Both are largely black with yellow or whitish metasomal bands and often limited marks on the head and thorax. Thus they resemble small vespids such as the *Odynerus* group of Eumeninae and the genus *Brachygastra* in the Polybiini (C.D.M. found *Eulonchopria*, leucospids, and *Brachygastra* on the same flowers at the Chamela Field Station). Wing folding enhances this resemblance to stinging wasps. For leucospids and male *Eulonchopria*, the mimicry would presumably be Batesian; for female *Eulonchopria*, it could be Müllerian or mixed Batesian and Müllerian because the female bees are equipped with strings as are the vespids. Figitine and eucoilid wasps are parasites of larval cyclorrhaphous Diptera living in dung, carrion, or decaying plant and fungal materials. As suggested by Vet & Alphen (1985) for *Kleidotoma*, it is possible that wing folding allows easier movement through the small holes and crevices in such materials. We can suggest no advantages for wing folding in the Gasteruptiidae. Wing folding in the pompilid genus *Poecilopompilus* is associated with mimicry of *Polistes* wasps (Belt 1874, 133–135; Evans 1968) and may enhance the similarity. The function of wing plaiting in the mostly black genus *Episyron* is less obvious; largely black vespid wasps might be models in some areas, but the predominance of mostly black coloration in the pompilids makes it difficult to strongly support the idea of mimicry in this case. The function of the weak fold line in other genera of Pompilinae is unclear, but it may play a role in wing shape changes in flight.

The theory of the importance of mimicry in explaining folding in *Eulonchopria*, leucospids, and *Poecilopompilus* is supported by the frequency of darkening of the costal part of the forewing in other insects that resemble vespids. Such darkening without folding produces a dark strip resembling the folded vespid wing, and to the human observer clearly enhances similarity to wasps. Groups that show such darkening and some of the species involved are as follows:

#### Hymenoptera

##### Ichneumonidae

*Metopius edwardsii* Cresson, *M. krombeini* Townes, *M. pulchellus* Cresson, *M. rileyi* Marlatt, *M. vittatus* Townes.

##### Sphécidae

*Cerceris binodes* Spinola, *C. chiriquensis* Cameron, *C. californica* Cresson; *Eucerceris* spp.

##### Colletidae

*Hylaeus maculipennis* (Smith); *Leioproctus eulonchopriodes* Michener.

#### Halictidae

*Neocorynura polybiodes* (Ducke); *Lastioglossum katyae* McGinley, *L. crocoturum* (Vachal).

#### Megachilidae

*Dolichostelis* spp.; *Anthodioctes megachiloides* Holmberg, *A. mapirensis* Cockerell; *Hypanthidium toboganum* Cockerell, *H. panamense* Cockerell; *Nananthidium tamaulipanum* Michener & Ordway; *Megachile* (*Ptilosarus*) spp.

#### Pompilidae

*Auplopus semialatus* Driesbach; *Poecilopompilus* spp. (also fold their wings).

#### Diptera

##### Syrphidae

*Ceriana* spp., *Sericomyia* spp., *Somula* spp., *Spilomyia* spp., *Temnostoma* spp.

##### Conopidae

*Conops magnus* Williston, *C. soror* Krombein; *Physocephala* spp.; *Physoconops* spp.

##### Stratiomyidae

*Hoplitomyia* spp., *Hermetia comstocki* Williston.

#### Neuroptera

##### Mantispidae

*Climaciella* spp.

#### Lepidoptera

##### Ctenuchidae

*Isanthrene fulvipuncta* Hampson, *I. aterrima* (Walker), *I. vespiformis* (Butler); *Eumengaster eumenes* Herrich-Schaeffer, *E. pseudosphecia* Hampson; *Sphecosoma mellissa* Schaus; *Pseudosphecia polistes* Huebner, *P. deceptans* Zerny, *P. laticinctus* Hampson.

In addition, some Sphingidae, many Zygaenidae, a few pyraustine Pyralidae, and some Thyrididae and syntomine Arctiidae have wings colored in a way that resembles those of vespid wasps (J. Rawlins, personal communication). Similarly, resemblance to plaited vespid wings is achieved in some wasp-mimicking sesiid Lepidoptera in which the forewing is largely dark and the hind wing clear. Examples are *Podosesia syringae* (Harris), *Vitaceae polistiformis* (Harris), *Hymenoclea palmii* (Beutenmüller), and *Melittia cucurbitae* (Harris). Finally, a number of wasplike ctenuchines actually fold their wings longitudinally (J. Rawlins, personal communication).

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