The Wing-Coupling Apparatus of Hemiptera Auchenorrhyncha: Structure, Function, and Systematic Value

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Abstract:

The main structure of the wing-coupling apparatus in the Auchenorrhyncha (Insecta, Hemiptera) has a wing-coupling fore fold (WCFF) on the claval margin of the fore wings and a similar, longitudinal wing-coupling hind fold (WCHF) or shorter wing-coupling lobe (WCL) or wing-coupling hook(WCH) on the costal margin of the hind wings. The shape and the size of the various parts of the wing-coupling apparatus, and the morphological differences of the microsculptures present on these, may be used as systematic characters at least up to generic level.

The main structure of this apparatus is similar to that in the Sternorrhyncha and instead, in the Coleorrhyncha is Heteropterous type: it has a complex structure on the fore wing ventral surface which grips a double longitudinal fold along the hind wing costal margin. The main structure of the wing-coupling apparatus could be useful to better understand the affinity among the different groups of Rhynchota.

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In evolved groups of Pterygota Insects, during the transition from the resting to the flight position, the movement of the fore and hind wings allows reciprocal wing coupling by means of the wing-coupling device so that the wings on each side function as a single unit.

The wing-coupling apparatus (WCA) consists of hooks, setae, spines, lobes, and folds displaced along the posterior margin of the fore wings and the anterior margin of the hind wings; these structures couple each other during flight and have different shapes in the various groups of Pterygota.

Within Homoptera, the arrangement of the coupling parts in the wing-coupling apparatus have one or more hooks in Sternorrhyncha and a lobe or a longitudinal fold in Auchenorrhyncha along the hind wing costal margin which grip a longitudinal fold in the fore wing posterior margin (Fig. 1).

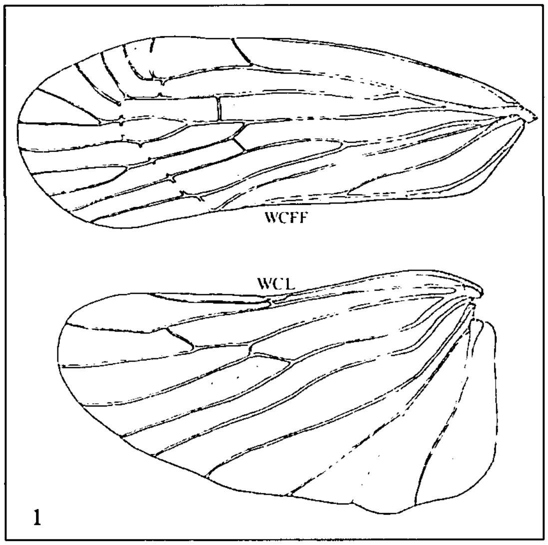


Fig. 1 Localization of the wing-coupling apparatus in fore and hind wing of *Malenia sicula* (Derbidae)

In Coleorrhyncha and Heteroptera, the arrangement of the coupling parts is different from that found in Homoptera, with a complex structure on the fore wing ventral surface which grips a double longitudinal fold along the hind wing costal margin.

The WCA in Auchenorrhyncha

Up to now, some authors have furnished little and then only generic information concerning the wing-coupling apparatus in Auchenorrhyncha but only few of them have given detailed information on this topic: OSSIANNILSSON (1950) was the first to carry out light microscope studies of the WCA in various families; SCHNEIDER & SCHILL (1978) gave data on a few species using SEM; D'URSO & IPPOLITO (1994) performed a detailed SEM study of 33 species belonging to 15 families showing the systematic and phylogenetic value of the WCA. In addition, WCA structure and function have been the topic in two M.S. by CHU (1971) and WOOD (1979).

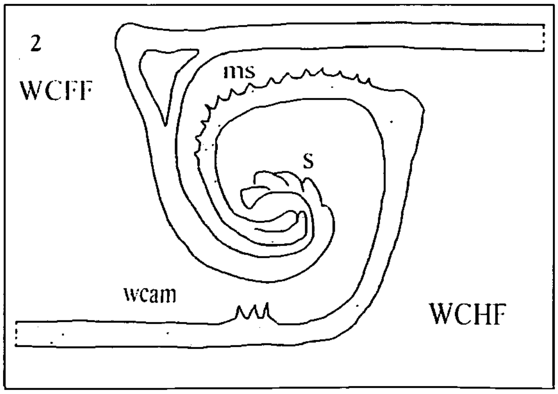


Fig. 2 Outline of the wing-coupling mechanism in Auchenorrhyncha. Fore wing in white and hind wing in black dots

The main structural plane in the WCA in Auchenorrhyncha always consists of a longitudinal fold along the claval margin of the mesothoracic (either tegmina or membranous) wings, called the wing-coupling fore fold (WCFF), and a similar longitudinal fold (the wing-coupling hind fold – WCHF), or short lobe (the wing-coupling lobe – WCL), or hook (the wing-coupling hook – WCH), on the costal margin of metathoracic wings.

In addition to the fold or lobe/hook on the metathoracic wings, microsculptures were constantly observed on one or more veins (ScP+R+MA trunk) and sometimes also on the wing membrane near the fold or lobe. They are called the wing-coupling accessory microsculptures (WCAM) (Figs 3, 5, 7, 8, 9, 10, 12, 13, 16, 19, 22). They were absent in the Cicadidae. These microsculptures are generally differently shaped or more numerous and more developed than those on the rest of the wing. These structures very likely play an active part in wing-coupling. Sometimes the WCAM are very small. In some cases, the wing portion near the fold represents only one of the densest areas of microsculptures, which cover the wing membrane (Figs 10, 13, 19). There is seldom no difference in ornamentation, compared with the rest of the wing.

The WCFF on the fore wing has a dorsal convexity on the wing margin, whereas the WCHF (WCL or WCH) are dorsally concave. The 2 WCA structures couple only when the wings open for flight, and when they are coupled, the convex part of the hind wing WCA is in contact with the concave surface of the forewing WCA. (Fig. 2)

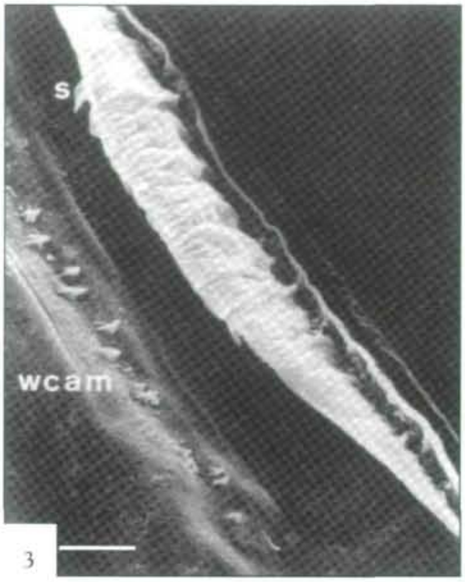
The WCFF structure (Figs 4, 6, 14, 18, 23, 26) is similar in all the families studied (Cixiidae, Dictyopharidae, Flatidae, Lophopidae, Ricaniidae, Issidae, Delphacidae, Tropiduchidae, Tettigometridae, Derbidae, Meenoplidae, Cicadidae, Cercopidea, Membracidae, Cicadellidae). In fact, it is an expansion of the posterior mesothoracic wing margin, it is ventrally folded and formed by the subterminal part of the jugal vein (DWORAKOWSKA 1988). It is always long, originates about half way along the wing margin, but never exceeds the apex of the claval furrow. The convex surface of the WCFF is always divided into 2 completely distinct longitudinal areas. The marginal area has longitudinal rows of generally imbricated flat microsculptures (shovels) and is almost always separated from the rest of the shovels' free folds by a prominent ridge (Figs 4, 6, 14, 23, 26). This ridge is absent only in Cicadidae (Fig. 18) and Cercopidae. The shovels sometimes have distally recurved and pointed apices; the proximal, distal and basal row shovels are generally modified and often spine-like (Fig. 4). Tiny microsculptures, microspines or wrinkles may be present on the convex shovel-free surface (Fig. 14).

The coupling area of the metathoracic wings is situated in the distal-third of the wing and has 2 main shapes: types A and B.

Type A apparatus consists of a lobe (WCL) (Figs 17, 19, 22, 24) stemming from the dorsal area of the costal margin. It twists upwardly and forms a spiral along the longitudinal wing axis. The distal tip of the lobe ends more sharply than does the proximal one. According to DWORAKOWSKA (1988), the WCL can be identified as the terminal part of the Praecosta, which fuses with both the costal veins (anterior Costa and posterior Costa) and forms the costal complex. Typical, flat, variously shaped or spine-like microsculptures are present on the convex surface of the lobe (Figs 17, 19, 22, 24). These structures are modified in the peripheral areas. The concave surface of the lobe is sometimes wrinkled. In the Typhlocybinae, the lobe is reduced to a hook (WCH) (Fig. 25) pointing towards the wing apex. Type A apparatus is found in Cicadidae, Cercopidea, Membracidae, Cicadellidae.

Type B apparatus (Figs 3, 5, 7-13, 15, 16) has the same site and relationship with the veins as type A. It consists of a nonspiral, longitudinal fold (WCHF) that resembles the WCFF, in that it is very long and presents longitudinal rows of shovels near its free margin. However, these shovels are not in an area separated from the rest of the fold by a proximal ridge. The shovels are similar to those observed in the WCFF, but are longer, incurved and point towards the wing apex (Fig. 7). The first row is generally modified and the shovels are smaller and different in shape to the others, whereas they become progressively longer in the more marginal rows. There may be ridges and microspines on the convex surface of the fold. The concave surface is sometimes wrinkled with evident ridges (Fig. 11). Type B apparatus is found in Cixiidae, Dictyopharidae, Flatidae, Lophopidae, Ricaniidae, Issidae, Delphacidae, Tropiduchidae, Tettigometridae, Derbidae, and Meenoplidae.

Figs 3-26 are reprinted from D'URSO V. & S. IPPOLITO (1994): Wing-coupling apparatus of Auchenorrhyncha (Insecta: Homoptera). — Int. J. Insect Morphol. & Embryol. 23(3): pp 211-224, with permission from Elsevier Science.



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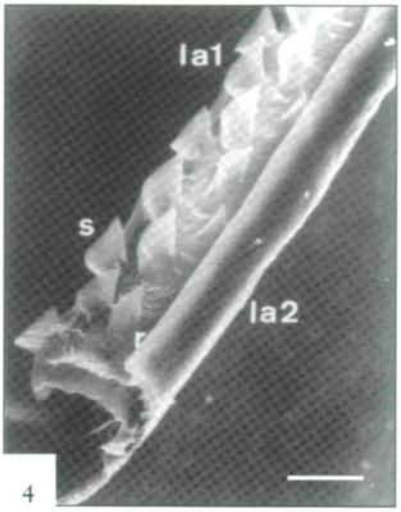

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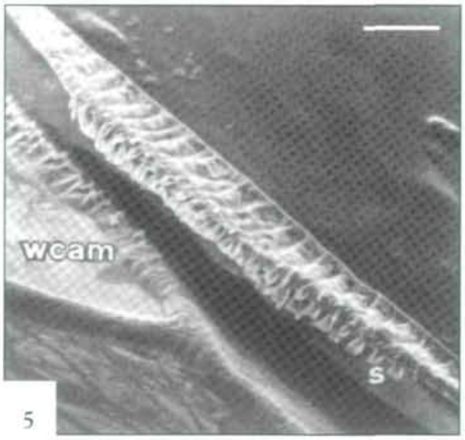

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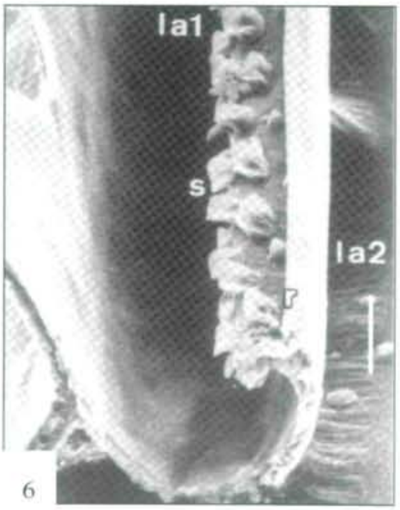

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When the resting position changes to the flying position, the movement of the fore wing on the hind wing allows wing-coupling via the WCA. The shape of the WC metathoracic structures (folds, lobes, hooks) allows them to slot into the WCFF at the start of flight, slide back and forth during flight and come out at the end of flight. Their spiral shape and marginal shovels permit greater adhesion between the fore- and hind wings during flight, and reduce the risk of early detachment when the WCHF (WCL or WCH) slide inside the

Fig. 3 Wing-coupling hind fold (*Hemitropis viridula*, Cixiidae). Scale: 18µm

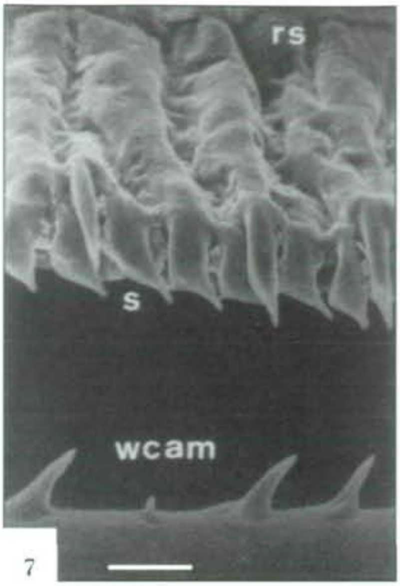
Fig. 4 Wing-coupling fore fold (*Reptalus panzeri*, Cixiidae). Scale: 8,6µm

Fig. 5 Wing-coupling hind fold (*Dictyophara europaea*, Dictyopharidae). Scale: 38µm

Fig. 6 Wing-coupling fore fold (*Dictyophara europaea*, Dictyopharidae). Scale: 14µm

WCFF. Spines, ridges, and flattened microsculptures on the convex surfaces of the WC meso- and metathoracic structures increase friction between the 2 surfaces. Microsculptures are found only on 1 of the 2 adhering, folded surfaces. The WCAM have similar functions.

According to D'URSO & IPPOLITO (1994), in all the cercopid and cicadellid species observed, in Membracidae, and in some Fulgoromorpha, 1 or 2 rows of sensilla are present along the costal margin of the metathoracic wings between the WCA and wing articulation. These sensilla have real bristles, are peg-like setae, and are probably involved in the perception of coupling and uncoupling movements of the wings. The Cercopidae have 2



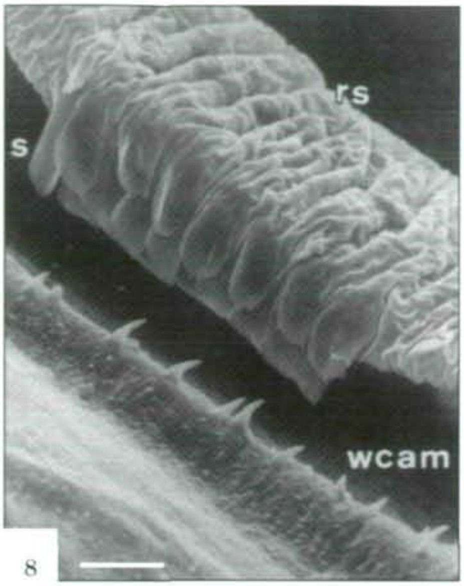
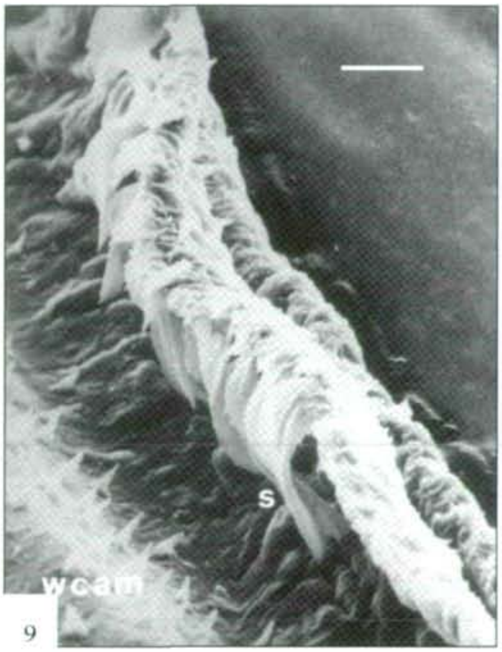
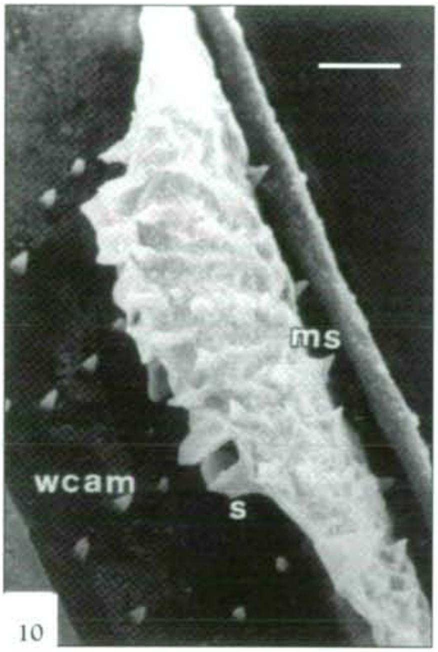
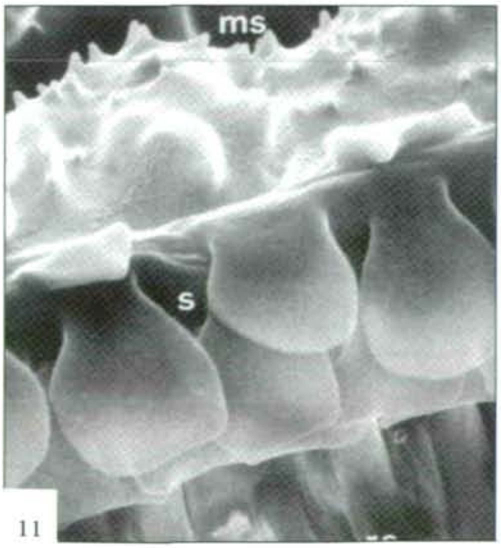


Fig. 7 Wing-coupling hind fold (*Lawana* sp., Flatidae): detail. Scale: 25µm

Fig. 8 Wing-coupling hind fold (*Phantia subquadrata*, Flatidae). Scale: 13µm







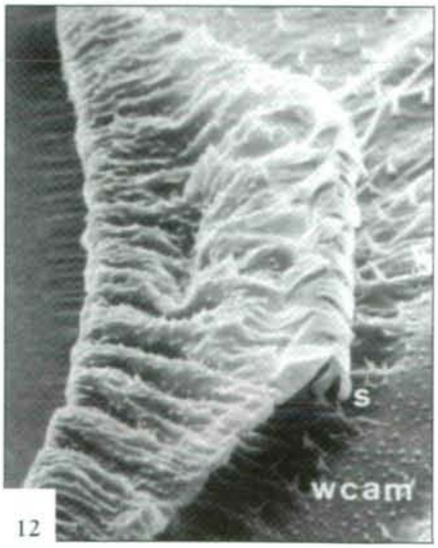


Fig. 9 Wing-coupling hind fold (*Ditropis pteridis*, Delphacidae). Scale: 6,6µm

Fig. 10 Wing-coupling hind fold (*Ommatissus* sp., Tropiduchidae). Scale: 15µm

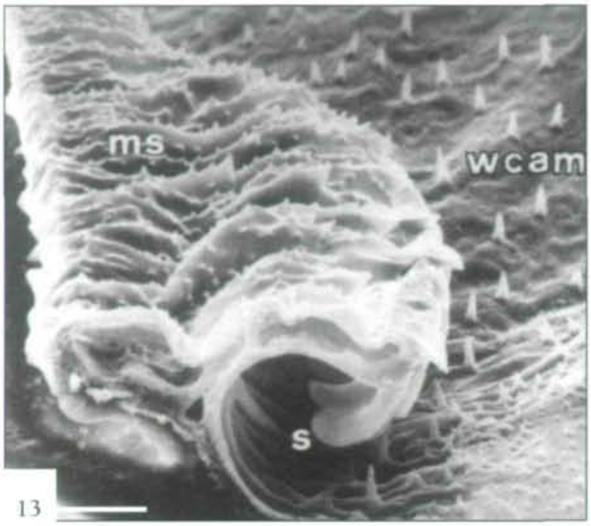
Fig. 11 Wing-coupling hind fold (*Brachyceps brachycephalus*, Tettigometridae) detail. Scale: 2,5µm

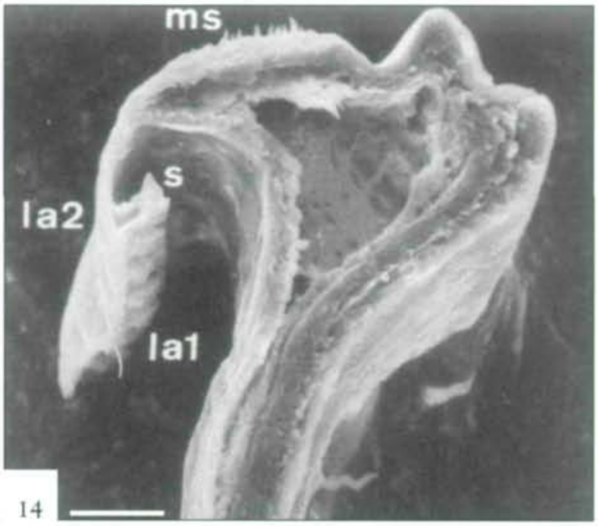
Fig. 12 Wing-coupling hind fold (*Brachyceps brachycephalus*, Tettigometridae). Scale: 10µm rows of sensilla, there being about 4-6 in the distal row, which are easily detected along the distal margin of a subtriangular expansion with a rounded apex. Each sensillum (Figs 20, 21) is made up of 2 articulated parts, dorsally folded and distally extended. They have an inner canal, and are innervated by a single cell whose extension ends at their bases (ZACWILICHOWSKI 1936). The shape and size of these sensilla are characteristic of the different species of Cercopidae. A similar wing expansion to that seen in the cercopid is also present in the flatid (with sensilla) and ricaniid species (without sensilla) observed. When the wings are coupled during flight, the expanded area touches the ventral surface of the forewing.

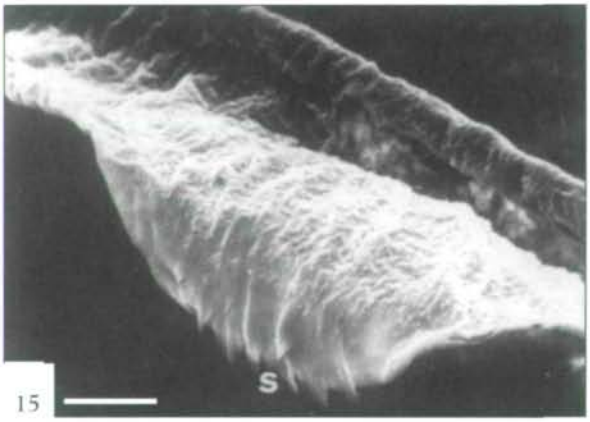
Examination of the WCA in the various Auchenorrhyncha groups reveals that the Fulgoromorpha have a rather uniform structural plane, and this agrees with the hypothesis of the monophyly of this group. In fact, all have WCHF (type B); WCAM, and their WCFF are not very different from WCHF, except that the shovels are on an area distinctly separated from the rest of the fold by a ridge.

Within the Fulgoromorpha, the Derbidae and Meenopliidae, differ most from the other families because their WCHF is reduced and tends to resemble type A (WCL) (with regard to shape, reduced size, small flattened, and sharp microsculptures, which also extend onto the convex surfaces and are not solely marginal). The WCHF is never spiral and often the vein opposite the fold has a WCAM made up of strong microspines, making it resemble the corresponding structure in the Heteroptera on the mesothoracic wing. Tropiduchidae, Delphacidae, and Tettigometridae, have a very similar coupling apparatus with short subtrapezoidal WCHF, transversely grooved concave surface, and ridges and microspines on the convex surface.

All the other families of Fulgoromorpha (Cixiidae, Dictyopharidae, Flatidae, Lophopidae, Ricaniidae, Issidae) are rather alike, with long WCFF covered in transverse ridges without microspines.







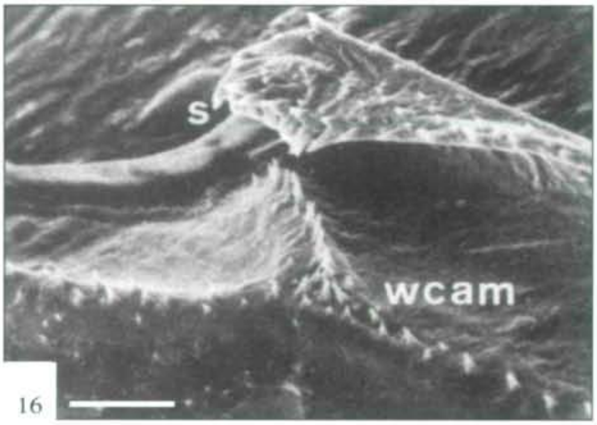


Fig. 13 Wing-coupling hind fold (*Brachyceps brachycephalus*, Tettigometridae). Scale: 7,6µm

Fig. 14 Wing-coupling fore fold (*Brachyceps brachycephalus*, Tettigometridae). Scale: 10µm

Fig. 15 Wing-coupling hind fold (*Malenia sicula*, Derbidae). Scale: 8µm

Fig. 16 Wing-coupling hind fold (*Diostrombus* sp., Derbidae). Scale: 27µm

The Cicadomorpha (Cicadidae, Cercopidae, Membracidae, Cicadellidae) have a type A coupling metathoracic apparatus, with spiral lobe and flattened microsculptures not only near the margin but also spread over part of the convex surface. One can regard WCA of type A as an apomorphic character; this gives value to the hypothesis that Cicadomorpha, having this synapomorphy, are a monophyletic strain, different from that of the Fulgoromorpha. The Cicadidae differ from the other 3 families in that it has a very long WCL, no WCAM and its WCFF closely resembles the WCL. Cercopidae and Membracidae have small, squarish WCL. In the Cicadellidae, the WCL varies greatly in shape. It may be similar to that seen in Cercopidae and Membracidae, or very reduced as in Typhlocybinae, where it resembles a hook (WCH). In Cercopidae, Membracidae, Cicadellidae, the WCAM are usually not very developed and, with the exception of the Cercopidae, the shovels in their WCFF are sited in a marginal area distinctly separated from the rest of the fold by a ridge.

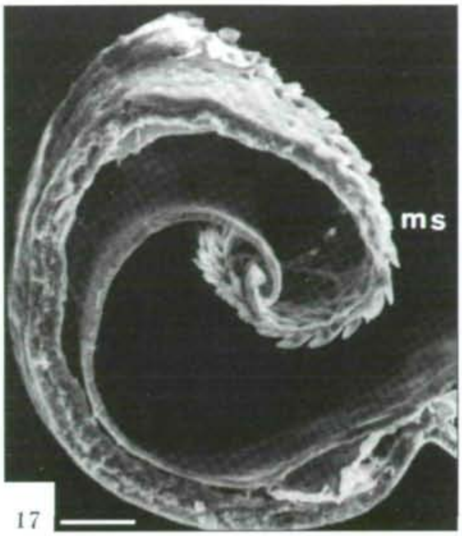
Fig. 17 Wing-coupling lobe (*Cicadatra atra*, Cicadidae). Scale: 21μm

Fig. 18 Wing-coupling fore fold (*Cicadatra atra*, Cicadidae). Scale: 27μm

Fig. 19 Wing-coupling lobe (*Cercopis sanguinolenta*, Cercopidae). Scale: 18μm

Fig. 20 Sensillum, hindwing (*Philaenus spumarius*, Cercopidae). Scale: 15μm

Fig. 21 Sensillum, hindwing (*Cercopis sanguinolenta*, Cercopidae). Scale: 8μm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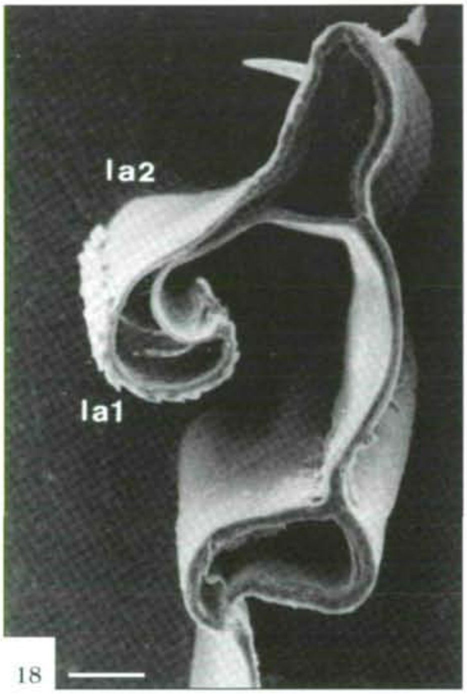
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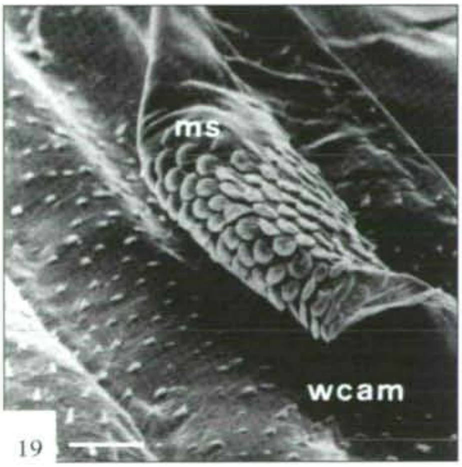
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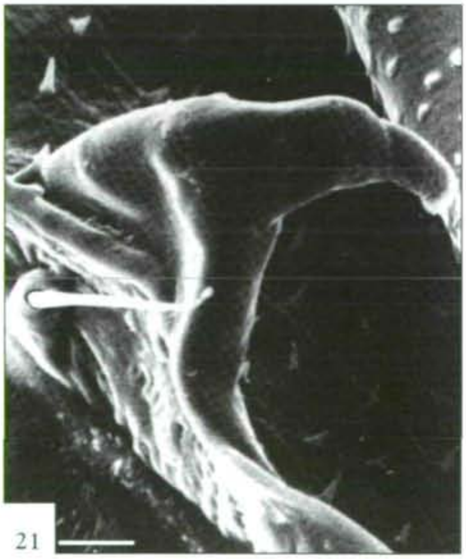
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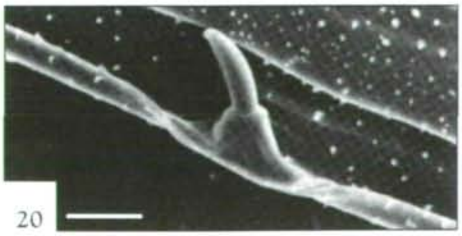
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In the Auchenorrhyncha, the structure of the wing-coupling apparatus supplies characteristics of taxonomic value. This is especially valid for families, because each of them has a uniform main base structure. Moreover, the morphology of the microsculptures on the folds and lobes (in addition to their size and shape) and the WCAM can be used as systematic characteristics for the genus, and probably also for species.

A close relationship was seen between the presence of a coupling apparatus and wing development and also flying capacity. In fact, the absence of this apparatus in some long hind-winged species (e.g., the Issidae species: *Issus coleoptratus* and *Hysteropterum maculipes*) is probably related to their evolution, which has favored leaping instead of flight. The apparatus is also absent in short-winged species (e.g., *Hemisphaerius* sp., brachypterous *Ditropis pteridis*) belonging to several different families.

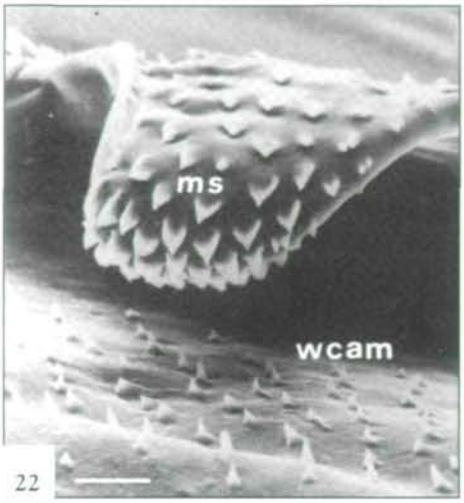
Comparison of the WCA in Auchenorrhyncha and in other Rhynchota

The main structure of WCA could be useful to better understand the affinity among the different groups of Rhynchota, comparing the one in Auchenorrhyncha and in the other groups traditionally assigned to Homoptera (Sternorrhyncha and Coleorrhyncha), and in addition, in Heteroptera.

The main structure of the coupling apparatus in the Auchenorrhyncha is similar to that in the Sternorrhyncha, where one or more spiral hooks generally replace the metathoracic lobe, which grasps a groove of the posterior margin of the mesothoracic wings.

The arrangement of the wing-coupling apparatus in the Coleorrhyncha is different; it has a complex structure on the fore wing ventral surface which grips a double longitudinal fold along the hind wing costal margin. (Fig. 27)

D'Urso (1993) gave detailed information at SEM in *Peloridium hammoniorum*, where the wing-coupling structure of the fore wings (FWC) (Fig. 28) is situated in the clavus near the apex on the vein that originates from the fusion of PCu and 1A. This structure has an internal and external part which are separated by a deep groove. The external portion (PO) (Figs 27, 28) is made up of a protuberance which is crowned by 4 or 5 series (25-30) of very long, flattened, round tipped and densely packed microsculptures. They are often directed inwardly and ventrally curved. One or two series of similar, but much shorter, microsculptures are present on the surface of the external protuberance, near the area where the longer ones arise from. The internal portion (PI)



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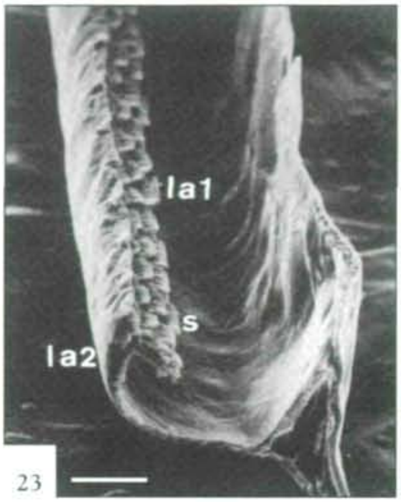

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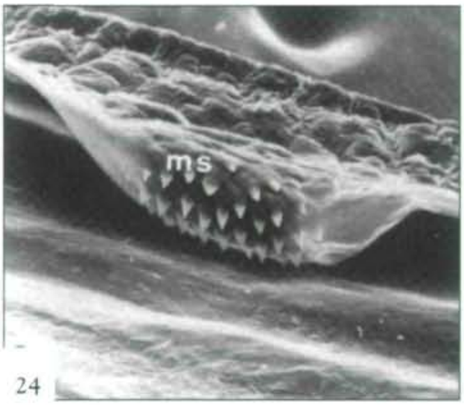

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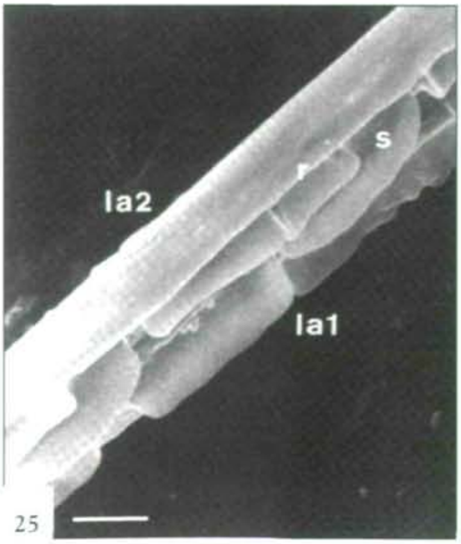
Fig. 22 Wing-coupling lobe (*Centrotus cornutus*, Membracidae). Scale: 12µm

Fig. 23 Wing-coupling fore fold (*Centrotus cornutus*, Membracidae). Scale: 16µm

Fig. 24 Wing-coupling lobe (*Selenocephalus obsoletus*, Cicadellidae). Scale: 14µm

Fig. 25 Wing-coupling fore fold (*Oncopsis tristis*, Cicadellidae): detail. Scale: 2,5µm

Fig. 26 Wing-coupling hook (*Fagocyba cruenta*, Cicadellidae). Scale: 2,1µm



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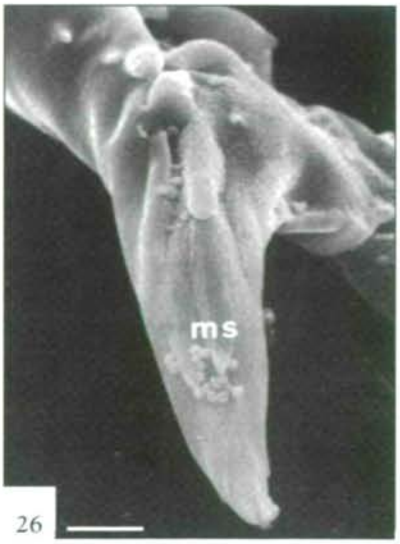

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(Figs 27, 28) lies opposite the external one and is separated by a groove (G) (Figs 27, 28). It is formed by a ridged area crowned by a group of about 20 spine-like, posteriorly and ventrally directed microsculptures. These are more curved than the external portion microsculptures. Rounded, apical-pointing, scale-like microsculptures are present nearer the apex of clavus.

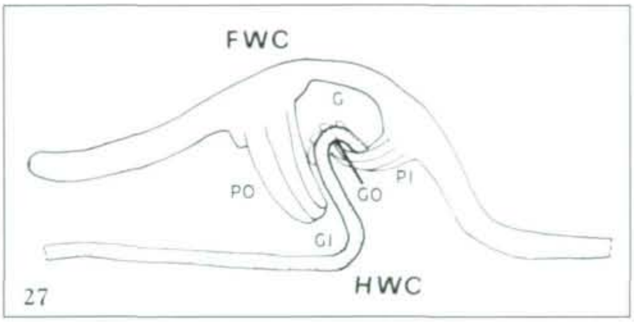

Fig. 27 Outline of the wing-coupling mechanism in Coleorrhyncha. Fore wing in white and hind wing in black dots (according to D'Urso 1993).

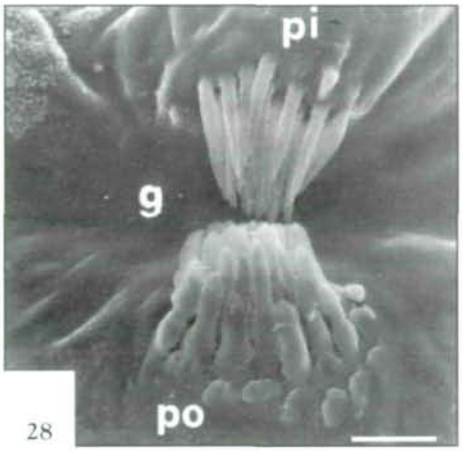

Fig. 28 Wing-coupling structure of the fore wing (*Peloridium hammoniorum*, Peloridiidae). Scale: 10µm

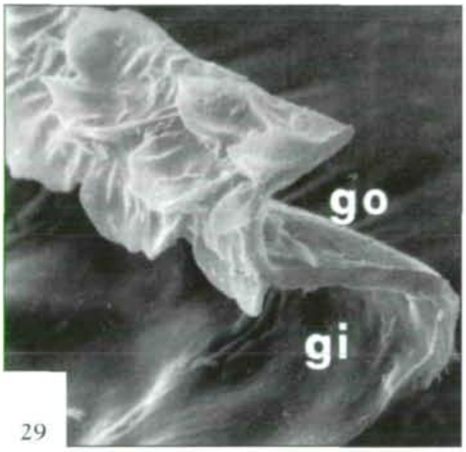

Fig. 29 Wing-coupling structure of the hind wing (*Peloridium hammoniorum*, Peloridiidae). Scale: 4,5µm

The hind wing coupling structure (HWC) (Fig. 29) is situated along the costal margin that forms a very long double longitudinal groove which arises proximally from the distal tip of the costa and ends at the level of posterior third of the wing margin. This longitudinal groove stems from a double curvature of the wing surface near the costal margin and has an S-shaped cross section. It folds internally and dorsally giving rise to a long inner groove (GI) (Fig. 29), before turning once again ventrally and externally to form another parallel outer groove (GO) (Fig. 29). Three-four series of scale microsculptures are found at the level of the convex surface of the external groove up to the free margin. They are either more or less halfmoon shaped or quadrangular. Their free margin is directed towards the interior of the wing. The proximal and distal tips of this fold are modified and tend to lose the double curvature; the scales become smaller, more simple and thinner. There are widespread, typical microsculptures on the wing membrane over the entire dorsal wing surface and near the double groove.

The fore wing coupling apparatus is so shaped that it grips the double metathoracic fold and slides back and forewards during flight before uncoupling at the end. The outer portion of the FWC runs along the inner metathoracic groove, while the inner portion slides along the outer one (Fig. 27).

No traces of wing coupling devices were observed on short wing specimens.

The wing coupling main structure observed in *Peloridium hammoniorum* greatly resembles the one present in Heteroptera. The FWC outer portion corresponds with Heteroptera "sliding head" (Schneider & Bohne 1977) or "Gleitkopf" (Schneider & Schill 1978), while the inner corresponds with their "sliding comb" (Schneider & Bohne 1977) or "Gleitkamm" (Schneider & Schill 1978). The double metathoracic fold corresponds with the similar structure on the Heteroptera's hind wing costal margin called the "S-shaped sliding fold" (Schneider & Bohne 1977) or "Gleitfalz" (Schneider & Schill 1978).

The differences are determined by the fine morphology of the various parts forming the coupling apparatus, i.e shape and number of microsculptures in the inner and outer portions of the FWC and the shape of the microsculptures in the HWC.

The arrangement of the coupling parts in the wing-coupling apparatus in *Peloridium hammoniorum* is different from the one found in Homoptera, in which the coupling portion is localized on the hind wing, and is always represented by one, or a series of, structures but never by two interlocking portions. In addition the coupled portion, localized on the fore wing, is always a plain fold and never S-shaped.

It must be stressed that the wing-coupling apparatus main structure is a constant character within large groups. Therefore, the Coleorrhyncha wing-coupling device main structure may support the hypothesis of the monophyly of Heteroptera and Coleorrhyncha, supported also by recent molecular data (SØRENSEN et al. 1995; CAMPBELL et al. 1995; CAMPBELL, STEFFEN-CAMPBELL, GILL 1995; OUVRARD et al. 2000). Although Heteroptera and Colerrhyncha on the one hand and Homoptera Auchenorrhyncha and Sternorrhyncha on the other have different structural planes, they are homogeneous within their own groups; this morphological data do not agree with molecular data based on 18S rDNA nucleotide sequences (SORENSEN et al. 1995; CAMPBELL et al. 1995; CAMPBELL, STEFFEN-CAMPBELL & GILL 1995; BOURGOIN, STEFFEN-CAMPBELL, CAMPBELL 1997) that show a paraphyly of Homoptera and of Auchenorrhyncha. According to these authors, within Hemiptera (Rynchota) there are four principal clades: Sternorrhyncha, Clypeorrhyncha (the Cicadomorpha), Archeorrhyncha (the Fulgoromorpha), Prosorrhyncha (the Heteroptera+ Peloridiidae); the Sternorrhyncha is a sister group to all others (called Euhemiptera); Archeorrhyncha is a sister group to Prosorrhyncha or Clypeorrhyncha but the most highly supported phylogenetic framework agrees with the first conclusion.

The morphological data concerning the WCA could agree with the phylogenetic framework of Rynchota inferred from molecular data only if we consider the main structure of WCA in Prosorrhyncha as an apomorphy: therefore, that hypothesis is not supported by the WCA structural plane of the Psocoptera that is the most primitive member of the hemipteroid orders.

Abbreviations used in figures

g = groove of FWC; gi = inner groove of HWC; go = outer groove of HWC; la1 = longitudinal area of WCFF with shovels; la2 = longitudinal area of WCFF without shovels; ms = microsculptures; pi = internal portion of FWC; po = external portion of FWC; r = ridge between longitudinal areas of WCFF, respectively with and without shovels; rs = ridges; s = shovels; wcam = wing-coupling accessory microsculptures.

Zusammenfassung

Der Mechanismus zur Flügelkoppelung bei Zikaden besteht vor allem aus einer vorderen Falte (WCFF) am Clavusrand des Vorderflügels und einer ähnlichen Längsfalte (WCHF) oder eines kürzeren Lobus am Costalrand des Hinterflügels. Gestalt und Größe dieser Teile des Flügelkoppelungsmechanismus und morphologische Unterschiede in den dort zu findenden Mikrostrukturen können als systematische Merkmale zumindest bis auf Gattungsniveau Verwendung finden.

Bei Zikaden entsprechen die wesentlichen Merkmalskomplexe jenen der Sternorrhyncha, während die Coleorrhyncha einen Flügelkoppelungsmechanismus vom „Heteropteren-Typ" aufweisen: eine komplexe Struktur im Bereich der Ventralseite des Vorderflügels, die in einer doppelten Längsfalte am Costalrand des Hinterflügels verankert wird. Merkmale im Bereich des Flügelkoppelungsapparates können einen wesentlichen Beitrag zum Verständnis der verwandtschaftlichen Beziehungen innerhalb der Hauptgruppen der Rhynchoten liefern.

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