Main Veins of the Wings of Auchenorrhyncha
(Insecta, Rhynchota: Hemelytrata [1]))

With 186 Figures

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Introduction

In accordance with the synthesized model of flying wing (KUKALOVA-PECK, 1983, Fig. 15) primarily there were 8 pairs of veins subbranched distally, each pair consisting of anterior convex (+) vein and posterior concave (—) vein and primarily each pair connected with a band of sclerites of its dorsal articulation.

All the previous attempts of constructing of the models of wing venation of the recent insects resulted in schemes speculated out of the same recent forms thus the circular reasoning was unavoidable when they were applied. Only when the hypothesized scheme would be based upon other sources it could meet the condition for real testing. Thus, if the above mentioned model of flying wing is based exclusively on fossils it provides the necessary condition. The aim of my study is to check if the hypothesized structures of the newest model of composite flying wing are demonstrated in the morphology of recent Auchenorrhyncha as it is examined true to fact.

Material

I have tried to obtain the insects which were referred to by the other authors (e. g. METCALF, 1913a, b, FUNKHOUSER, 1913, FENNAH, 1944, SHCHERBAKOV, 1981). However, in order to examine the full diversity of the structures I used also some other material, part of which could not be identified. Although it is not a custom in such a type of study, the documentary specimens are deposited in the Department of Entomology of the British Museum (Nat. Hist) and in the Staatliches Museum für Tierkunde Dresden for sake of verification. The source of the identification is provided in the square brackets, e. g. [H] means "det. K. G. A. HAMILTON", [W] "M. R. WILSON", [O'B] "L. B. O'BRIEN", [V] "C. A. VIRAKTAMATH". When such information is missing the identification is mine.

F u l g o r o i d e a . Issidae: *Colpoptera carlota* MYERS [I. C. MYERS], *Hysteropterum cornutum* MEL. [J. F. BRIMLEY], *H. asiaticum* LETH. [A. F. EMELJANOV], *Tylanira bifurca* BALL [O'B], *Osbornia arborea* BALL [O'B], *Issus coleoptratus* (F.) [W. WAGNER], *I. muscaeformis* (SCHR.), *Mycterodus confusus* (STÅL) [?],*Delhina* [H], *Brahmaloka* [H], *Sivaloka* [H], *Picumna* [H], *Ulixes* [O'B], *Thionia, Nubithia* [O'B], *Gengis panoplites* FEN., paratype and a new material (now *Acrometopum* STÅL), *Redarator bimaculatus* DIST., *Durium, Colmadona testudinaria* (DIST.), *Chlamydopteryx*. Acanalonidae: *Acanalonia* [H], *Hemithiscia*. Nogodinidae: *Neaethus* [O'B], *Neotylana* [from Nigeria — H], other species from S. Africa, *Hemispherius* [from Nigeria — H], *Dictyonissus griphus* UHL. [O'B], *Gaetulia vulgaris* CALDW. [O'B], *Dyctidea angustata* UHL. [O'B], *Dictyobia permutata* UHL. [O'B], *Varcia*. Lophopidae: *Pyrilla* [V], *Elasmoscelis stali* DIST. Ricaniidae: *Ricania fenestrata* (F.) [V]. Flatidae: *Ormenis, Juba plagosa* (DIST.), *Massila, Flatoides, Dalapax*, unidentified genera from S. Africa. Tropiduchidae: *Tambinia* [V], *Tropiduchus asturco* FEN. (paratype), *Numicia* [W], *Ommatissus binotatus* var. *lubica* DE BER. [W], *Trypetimorpha fenestrata* A. COSTA [W], *Pelitropis rotulata* VAN D. Eurybrachyidae: *Eurybrachys venusta* STÅL [O'B], *E. tomentosa* (F.) [V], *Paropioxys* [C. HEGERT], two unidentified Australian genera. Fulgoridae: *Laternaria* [H], *Hypaepa illuminata* DIST.

[1]) Hemelytrata FALLÉN, 1826

[O'B], *Scaralis* [O'B], *Phrictus minutacanthus* CALDW. [O'B], *P. quinquepartitus* DIST.
[O'B], *Cathedra serrata* (F.) [O'B], *Mamatola* [O'B], *Copidocephala* [O'B], *Odontoptera
carrenoi* SIGN. [O'B], *Enchophora* [H], Dictyopharidae: *Dictyophara* (a few species from
Americas and S. Africa), *Scolops* [H], *Nersia* [H], *Phyllosccelis* [O'B]. Achilidae: *Epiptera
pallida* SAY [H], *Rhotala* [O'B], *Ipsnola,* ? *Elidiptera,* ? *Koloptera,* ? *Ateson consimile*
FEN., several genera from S. America and S. Africa. Achilixiidae: *Achilixius* [W]. Derbidae:
Otiocerus degeerii KIRBY [H], *Patara vanduzei* BALL [H], other species of *Patara, Anotia
burnetii* FITCH [H], other species of *Anotia, Levu, Saccharodite, Mysidia, Muiria* (from
S. Africa), *Zoraida bohemani* (WESTW.), *Neocenchrea, Omolicna, Herpis, Persis (Ana-
persis),* several very different species of *Cedusa.* The genera of Cenchreini were identified
with the aid of key by O'BRIEN (1982). Meenoplidae: *Meenoplus* [V], *Nisia nervosa*
(MOTSCH.) [W], *Anigrus sordidus* STÅL. Kinnaridae: *Kinnara* ? *fumata* (MEL.) [W], *Epar-
menoides.* Cixiidae: *Oliarus* [H], *Cixius* [H], *Bothriocera,* several genera from S. America.
Delphacidae: *Ugyops* ? *taraculae* (MUIR), *Perkinsiella,* ? *Eucanyra,* several genera from S.
America and S. Africa, Tettigometridae: *Hilda patruelis* (STÅL) [Brit. Mus.], *Tettigometra*
? *sulphurea* M. R. [Brit. Mus.]. Caliscelidae: *Ommatidiotus dissimilis* (FALL.) [A. F. EMEL-
JANOV], *Peltonotellus histrionicus* STÅL [H], *P. nigroviridia* (BALL) [H], *Raphiophora*
(two species from the Philippines) [H], *Caliscelis* [V], several genera from S. Africa.

C i c a d o i d e a. *Tettigarcta tomentosa* WHITE [Austr. Mus.], *T.* ? *crinita* DIST., *Platy-
pleura divisa* (GERM.), *Calopsaltria longula* (STÅL), ? *Taipinga, Cyclochila australasiae*
DON. [Austr. Mus.], *Lyristes pruinosa* (SAY) [H], *Magicicada septendecim* (L.) [T. E.
MOORE], *Okanagana* [B. P. BEIRNE], *Polyneura* (from Nepal) [H], *Melampsalta, Chonosia.*

C e r c o p o i d e a. *Prosapia bicincta* (SAY) [H], *Locris, Ptyelus flavescens* (F.) [Transv.
Mus.], *Aphrophora* [H], *Philaenus spumarius* (L.) [H], *Philaenarcys bilineata* (SAY) [H],
Lepyronia quadrangularis (SAY) [H], *Clastoptera obtusa* (SAY) [H], several genera from
S. America and S. Africa, unidentified genus of Machaerotidae.

C i c a d e l l o i d e a. *Acutalis tartarea* (SAY) [B. P. BEIRNE], *Ceresa bisonia* (KOPP et
YONKE) [H], *Gerridius scutellatus* FOWL. [Brit. Mus.], *Platycotis,* several genera of Mem-
bracidae from Australia, S. America and S. Africa, *Holdgatiella* [H], *Darthula hardwickii*
GRAY [H], *Tropidaspis carinata* F. [Brit. Mus.], *Melizoderes, Bothrogonia ferruginea* (F.)
[Brit. Mus.], *Coloborrhis corticina* (GERM.) [H], *Aulacizes, Dichrophleps, Draeculacephala*
[H], *Ciminius hartii* (BALL) [H], *Ponana* [H], *Stenocotis depressa* WALK. [J. W. EVANS],
Athysanus argentarius METC., *Balclutha, Macrosteles, Idiocerus, Diomma pulchra* (MATS.),
Kamaza reducta DWOR., *Kyboasca bipunctata* (OSH.), *Joruma, Eurymela* [H], *Jikradia*
[H], *Agalliopsis* [H], *Xestocephalus tessellatus* VAN D. [H], *Hylica* [Brit. Mus.], *Balala*
[Brit. Mus.].

Method

Making comparative morphology the basis of phylogenetic research is possible only when
studied characters are soundly classified in accordance to their polarization in the
historical development of the group as it has been shown by HENNING (1981).
The first steptoward that is establishing homologies. The commonly comprehen-
ded definitions say that homology is the occurrence of the same structure (although it
might be differently manifested) in different organisms, or the inheritance of the same
structure by different organisms from the common ancestor; and the homologous structu-
res in different organisms are these which have been inherited from the common ancestor.
In other words the presence of homologous structures in different organisms provides
evidence of their common origin or affinity. Serial homology refers to structures which
though different segmentally have the same evolutionary origin. The term has been called
"misnomer" by DE BEER (1971) because seemingly it does not fit the Darvinian definition,
e. g. for the antenna and leg of the same specimen, considered as serially homologous,

Figs. 1—12.   ►
Fulgora: 1: diagram showing mode of development of pc cell and Pc+CP composite vein
in the fore wing (after FENNAH, 1944) — 2: *Enchophora,* costal margin (corresponding to
the 2nd cross-section shown in Fig. 1) — 3: *Tettigometra sulphurea* (F.), costal margin
(corresponding to the 2nd cross-section shown in Fig. 1) — 4: *Oliarus,* subbasal cross-
section through the costal margin — 5: *Oliarus,* cross-section at the level of the basal
curvature of CuA — 6: *Tettigometra sulphurea* (F.), cross-section through the costal margin
in the middle of the fore wing — 7: *Ormenis,* costal margin and the axial unit (correspond-
ing to the 4th cross-section shown in Fig. 1), compare with Fig. 175 — 8: *Eurybrachys,*
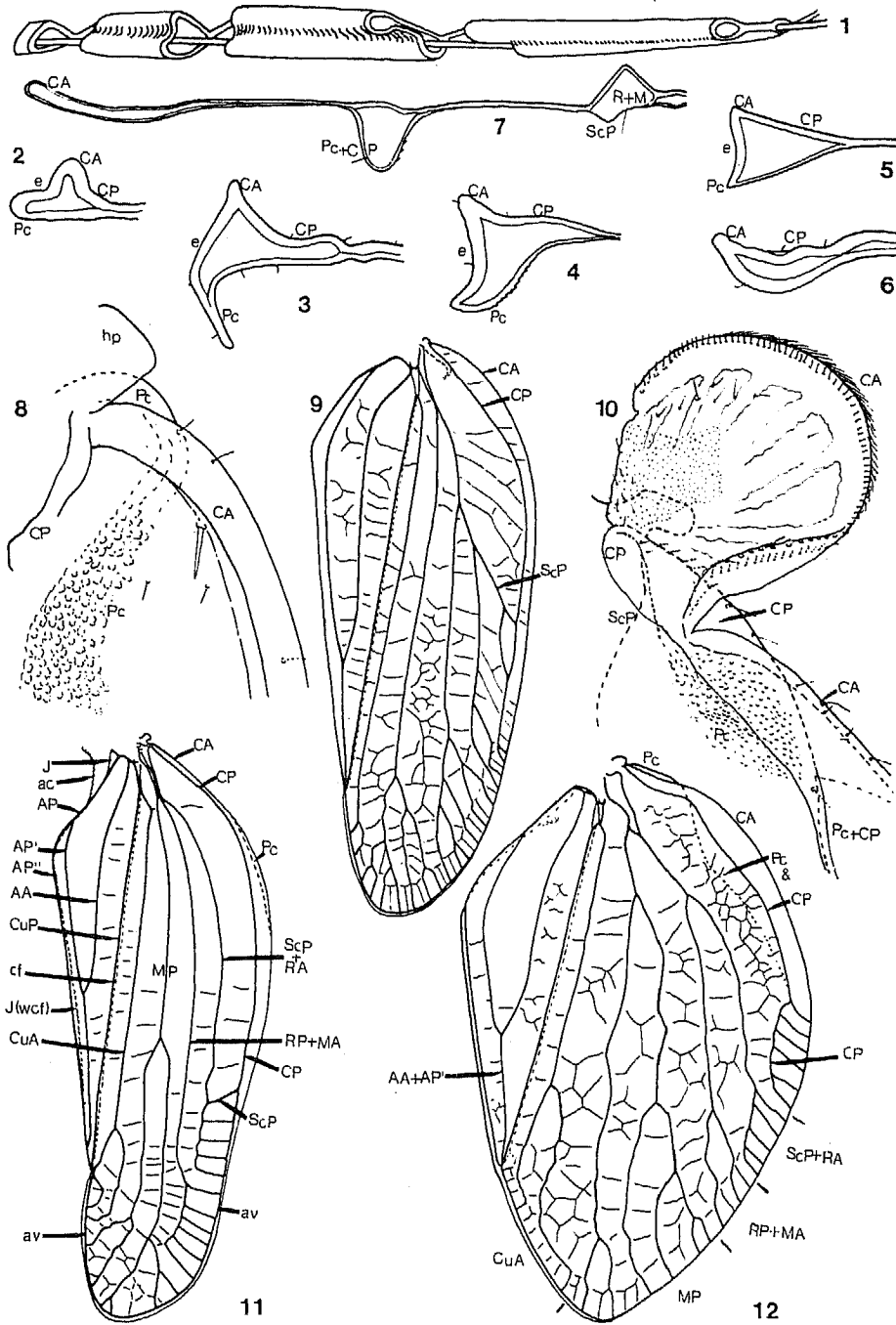
basal attachment of veins of the costal complex in the fore wing — 9: *Delhina*, fore wing (compare with Fig. 172) — 10: *Neotylana*, basal attachment of veins of the costal complex with the outline of the ScP to the left; CA forming a sensory organ at the base of wing — 11: *Colpoptera*, fore wing (Fig. 171 shows veins of the costal complex photographed from the edge where Pc ends) — 12: *Colmadona testudinaria* (DIST.), non flying fore wing (Pc is originally vertical at the very base as visible in Figs. 173 and 174).

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Entomol. Abh. Mus. Tierkd. Dresden 52, Nr. 3 (1988)

must not be necessary believed as linked with each other in the process of historical development. However, if serial homology is understood not as a derivation from the immediate ancestor but through the ancestral structure present at the base of phylla, the term remains both truthful and useful in the phylogenetic study of Arthropoda. The origin of metamery is still not a resolved problem despite many contradictory theories. But if metamery of Annelida results from multiplication of a basic unit and that of Chordata by means of subdividing, the term serial homology could be applied to the serial appendages of Arthropoda while its criticism in relation to the limbs of Vertebrata as DE BEER (1971) has done would be fully justified. The synchronous segment formation in insects might be cenogenetic and this should not undermine the above reasoning for as DE BEER, himself embryologist, denounced the value of details of embryological development in establishing homology, so do many other scholars.

When homologization of structures through the whole taxon under study is completed cladistic analysis is possible and that finally could lead to the reconstruction of phylogenesis. Hence, the basic task would be to find out the homologies. However, the above definitions of homology — homologous structures do not contain criteria and these were too often based on intuition through the "method" of trials and errors.

The most complete explanation of the principles of homologization referring to morphology is in the works by REMANE (1956, 1961 — in MATSUDA, 1976). The author distinguishes three major criteria and three minor (subsidiary) criteria as follows.

Major:
1. Position of a structure relative to neighbouring structures. There must be considered also: fusions, subdividing, reductions, loss or shifting in the position.
2. Outstanding characteristics of a structure.
3. Intermediate conditions of a structure.

Minor (subsidiary):
1. Probability that the structures are homologous increases if they occur in large number of related species.
Corrugation of the ambient vein in hind wing of Derbidae and deletion of the same in some of them helped to recognize correctly the origin of the unusual organ (FENNAH, 1944).
2. Probability that the structures are homologous increases with the presence of other homologies in the compared organisms.
The number of unquestionably homologous structures within Auchenorrhyncha is enormous but only these which are differently manifested in certain groups are the subject to scrutiny. This is why there is a common agreement as to the statement that Auchenorrhyncha are well defined group.
3. Probability that the structures are homologous decreases with frequency of occurrence of these characteristics in unrelated organisms.
The Pc+CP vein (Fig. 7) can serve as an example. It occurs constantly or diversely within several families of Fulgoroidea, in some Cercopoidea, Miridae, Tingidae and some other families of Heteroptera but also in Cassidinae of the Chrysomelidae beetles and in some other families of Coleoptera. Thus the structures are not likely to be homologous.
The subsidiary criteria of homology refer to taxonomic units but applying them will not lead to circular reasoning if the systematic arrangement of the subjected animals was based on other structures than these which homology is currently under examination and this is the case of Rhynchota.

Major Ad 1. In the present study the most important appeared to be linking of the veins with the row of sclerites of their dorsal articulation. The importance of that connection for the homologization of veins was emphasized by SNODGRASS (1935). Even preliminary examination indicates that it is hard to maintain the scheme of the three axillary sclerites of articulation as entities (for the opposite view see EMELJANOV, 1977). There is still
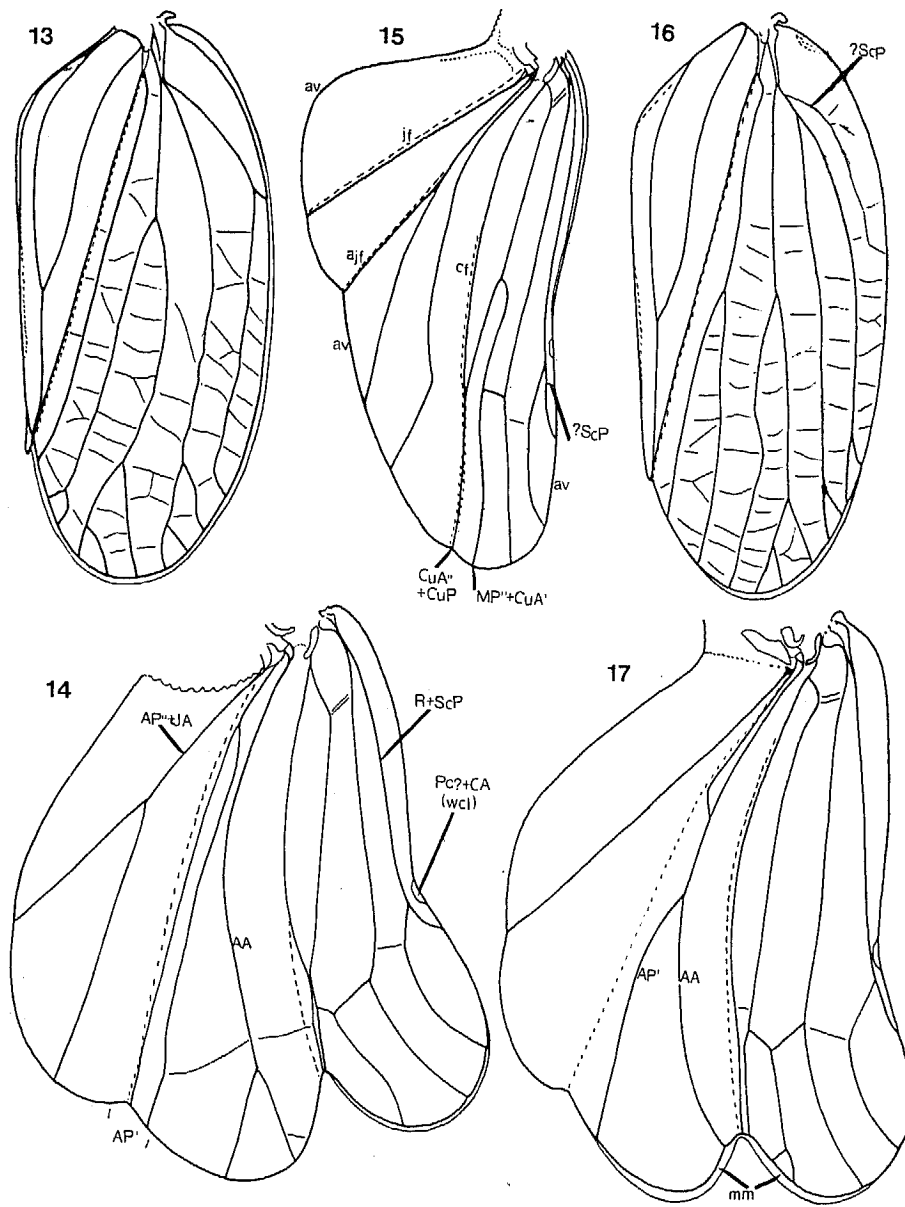
Figs. 13—17.
Thionia: 13: fore wing — 14: hind wing — *Colpoptera:* 15 — *Redarator bimaculatus* DIST.: 16, 17.

lack of the common agreement as to what the vein is? In the present study the primary vein is deemed to be a mechanical unit associated with its sclerites of dorsal articulation and most frequently containing also the haemolymph channel. Tracheae and nerves are not necessary components and it can not be accepted any longer that the "true" veins differ from the others by containing a trachea. Also it should be said at this point that veins can not cross each other and can not loose their lumen proximally at the same time retaining it distally. On the other hand the veins that shifted at margins becoming ventral

(but not the ventral (—) veins) or dorsal can change their position quite independently on the subsequent veins whether they are (+) or (—).

Major Ad 2. The most distinctive landmarks in the wings of Auchenorrhyncha include the sculpture on the ventral side at the base of Pc (Fig. 182), presence of the first trachea in CP, chitinous sensillae or details of the cuticular sculpture (HESLOP-HARRISON, 1955b), muscle insertions to the particular pteralia of dorsal articulation (Pc+CF, CuF), cu—m cross vein in the hind wing, the claval furrow and the cubital triangle in the fore wing and fluting at the very base of the fore wing.

Major Ad 3. The 94 identified genera of 19 families of Fulgoroidea used in this study were subject to an intensive and very detailed comparison from this point of view. Subsequently the results were extended to the other superfamilies. The third major criterium of homology was the one used the most frequently and theoretically it must always apply if to include sufficient number of related forms both recent and fossil.

Techniques

Insects preserved in 70 % ethanol, air mounted wings, total wings mounted in Canada Balsam, Euparol or Hoyer's medium were examined using dissecting as well as transmitting microscopes. Paraffine cross-sections 5—20 μm stained with Haematoxylin-Eosin or simple razor cross-sections of larger wings were also made. In a few cases haemolymphocytes were stained with Methyl Blue. There was one observation made of haemolymph circulation and similar equipment as that described by ARNOLD (1964) was used.

All wings and their parts are illustrated in dorsal view as right wings with their basal region upwards or to the left except when stated otherwise. The cross-sections show costal region to the left. Labeling follows the pattern suggested in Fig. 14 by KUKALOVA-PECK (1983), cross-veins are shown as disconnected. Additional explanations used in illustrations: ac — axillary cord, ajf — anojugal fold, av — ambient vein, b — brace, cf — claval furrow, ct — cubital triangle, cv — cross-vein, e — epipleuron, hp — humeral plate, iv — intercalary vein, jf — jugal fold, mm — marginal membrane, nl — nodal line, wcf — wing coupling fold (J), wcl — wing coupling lobe (Pc?+CA).

Results

Pronating unit — costal complex

The very anterior part of wing contains three veinal elements which are strongly associated with each other at least by their bases and hinged to the "humeral plate". The "humeral plate" is a part of the articulation band of these veins and it is separated from them by a desclerotized flexible junction (larger in fore wing). Basivenalia are fused to these veins. The pronating movement of the costal complex in the fore wing plays an indispensable aerodynamic function while that of the hind wing facilitates grasping of the anterior part of the wing coupling apparatus. Atlhough pronation is always counterbalanced by supination, the first accompanies forward movement and therefore it is emphasized in the name of the unit. The costal complex also has the function of protecting the metathoracic spiracles (in all but Cicadoidea) and fastening the fore wing to the pleuron at rest. The hind wing marginal vein forms a device for wing coupling during flight. The three veins are separated from the following veins by an area of membrane that is quite large in the fore wing and bordered posteriorly by a longitudinal line of flexion. In the hind wing the dividing space is often reduced and the postcostal flexion line is obscure.

Fore wing

Fulgoroidea. Praecosta (Pc)

Primarily this is the first vein of the costal complex. In Tettigometridae it forms a distinct, broadly arcuate lamella directed latero-ventrad, at the very base this vein retains an additional sinuated ridge running more ventrally (Fig. 86). The ridge might represent an anterior component (?PcA) while the more lateral part might be interpreted at the very base as PcP despite its elevation. Both parts become unified very soon. The lamellate Pc
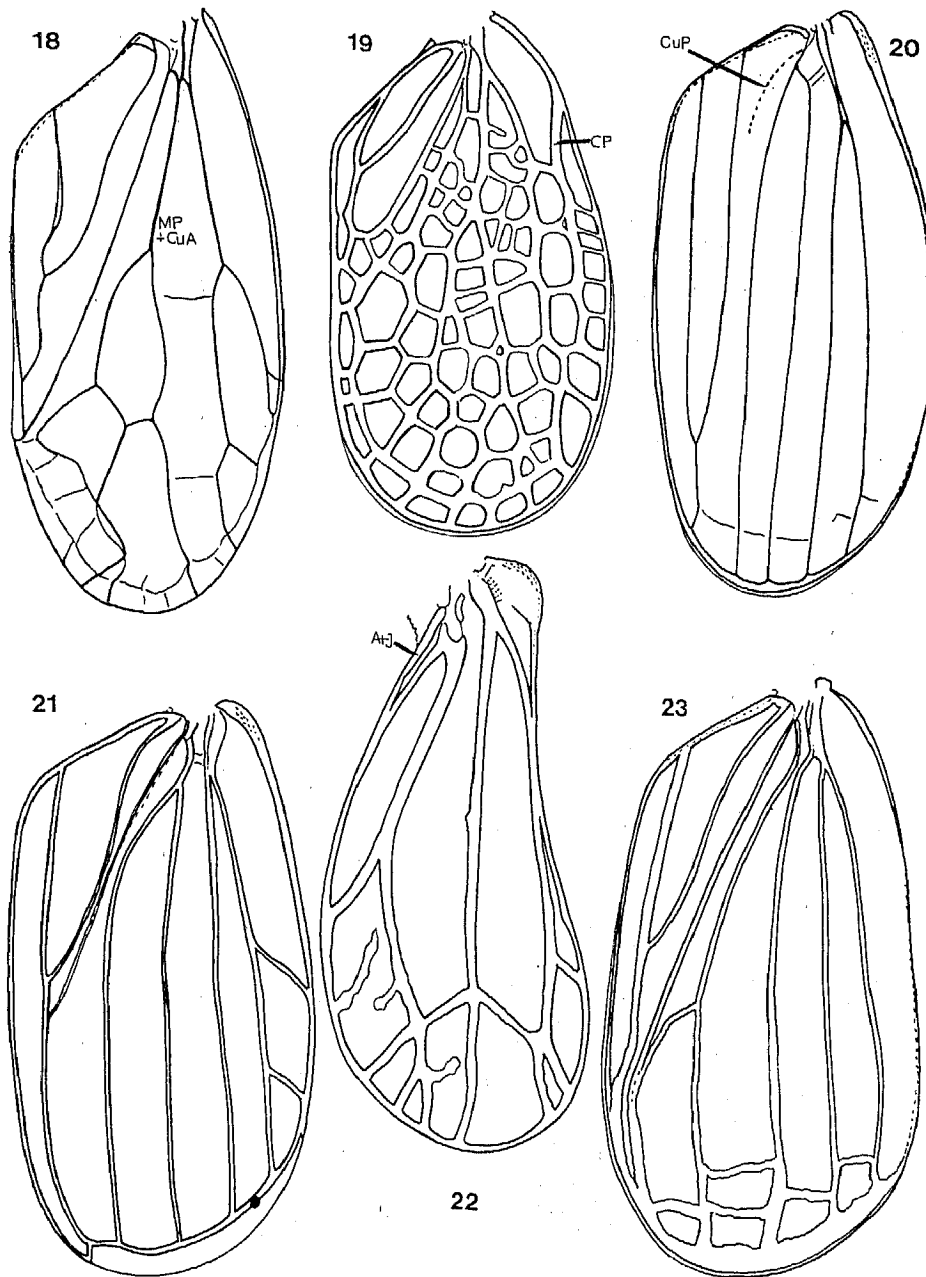
Figs. 18—23.
Non-flying wings. — *Acrometopum*: 18 — *Nubithia*: 19 — Issidae g. sp. (S. Africa): 20, 21 —
*Durium*: 22, 23.

is observable also in some Issidae e. g. *Hysteropterum, Sivaloka* (Fig. 170) and in *Epar-
menoides* of Kinnaridae. In the fore wing Pc has very distinct landmark — the field of
scales near the base on its ventral side, the scales are directed inward (Fig. 182). This
character of Pc is present in all Fulgoroidea with the exception of Meenoplidae, Derbidae
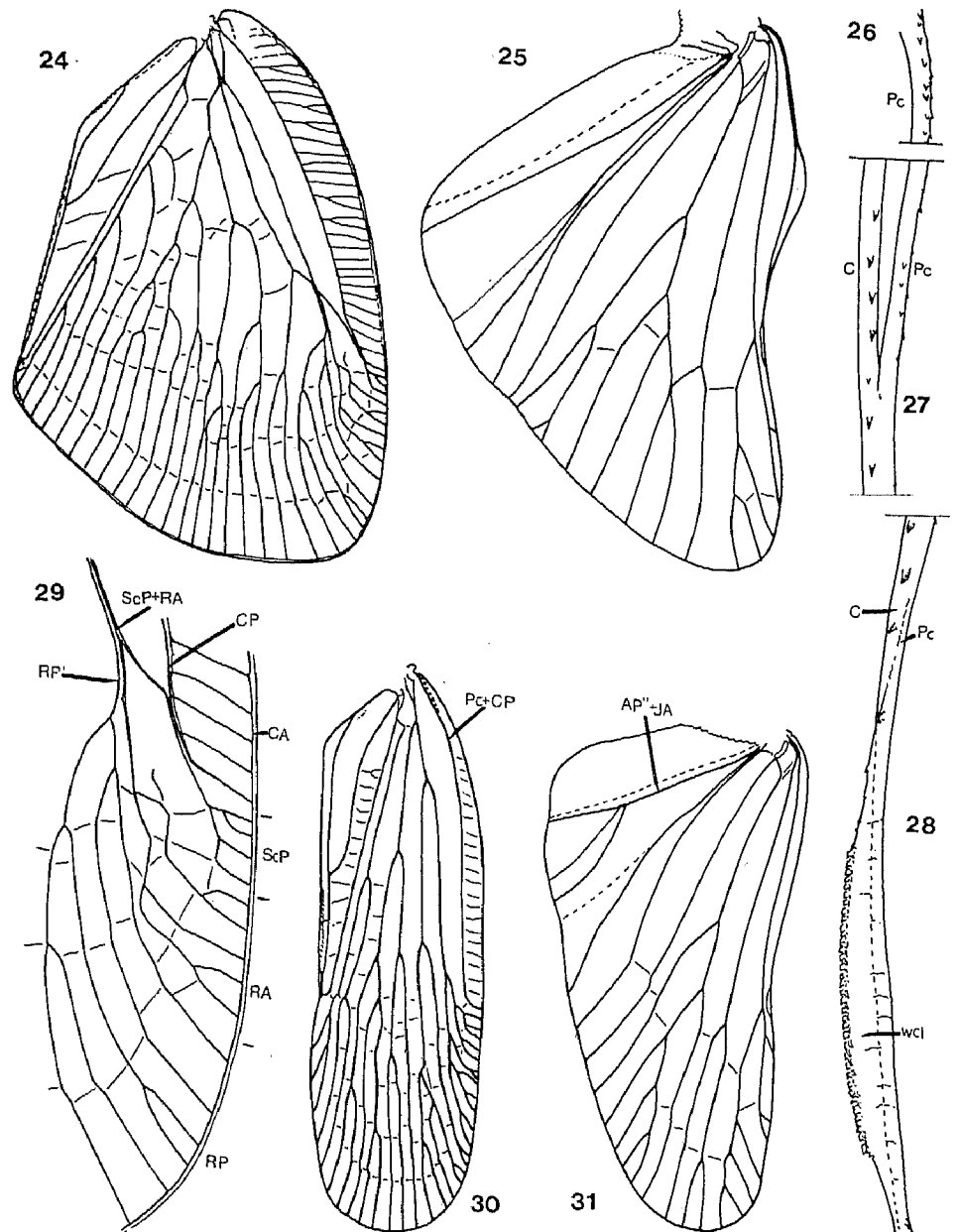
Figs. 24—31.
Ricania fenestrata (F.): 24—29. — 29: region of the costal nodus in higher magnification —
Pyrilla: 30, 31.

having veins of the costal complex similarly reduced at base, *Ricania fenestrata* (F.) and per-
haps all Ricaniidae. In most of wings Pc is fused wit both costal veins forming a very strong
composite vein at the costal margin. In such association Pc is more or less expanded
latero-ventral and more or less sharply terminated in a form of a ridge that in a cross-
section is an angulate ventral extension of the common haemolymph channel (Figs. 3—5).
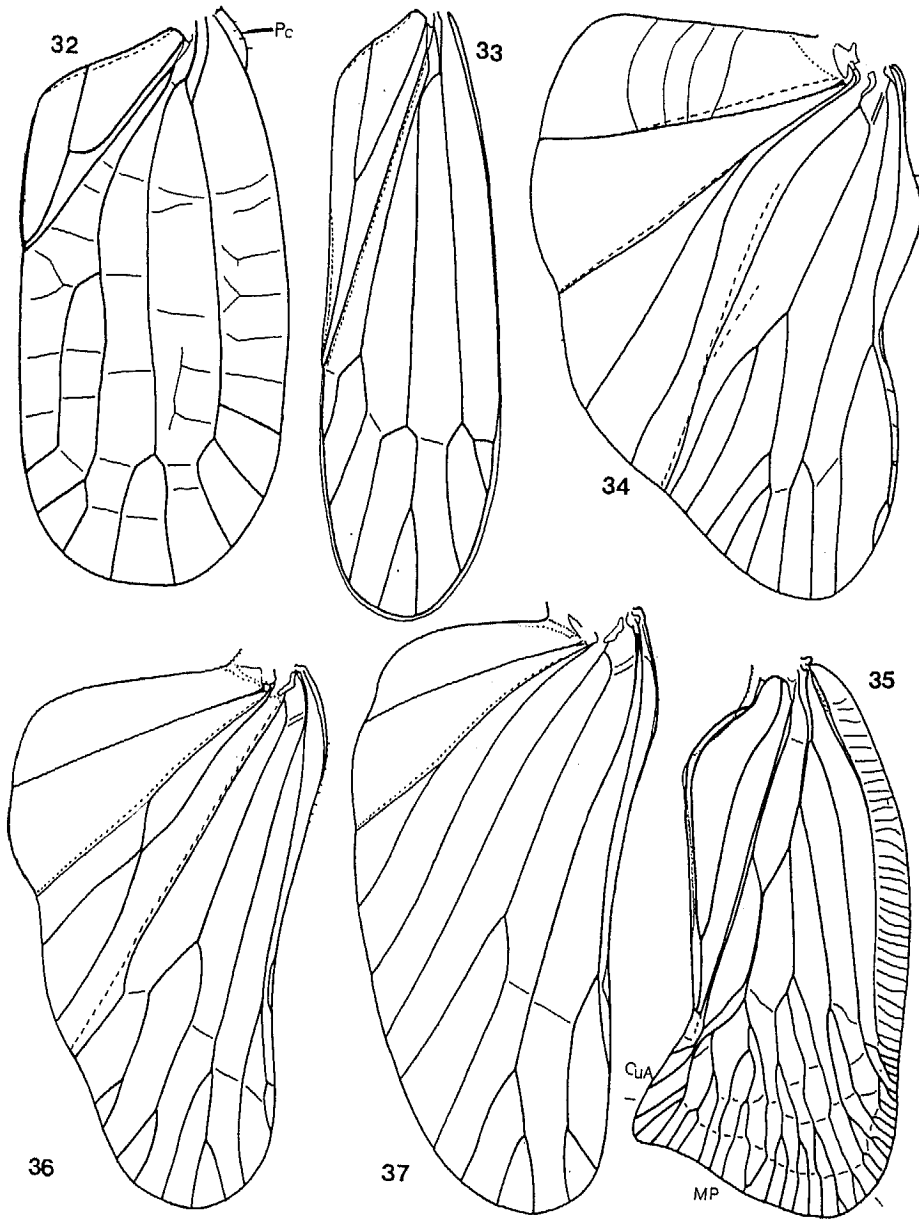
Figs. 32—37.
Trypetimorpha fenestrata A. COSTA, non flying wing: 32 — *Ommatissus binotatus* PUNBR.:
33 — *Juba plagosa* (DIST.): 34, 35 — *Pelitropis rotulata* VAN D.: 36 — *Numicia*: 37.

The protruding ridge is the only detectable sign of the presence of Pc beyond the very
base. The lateral surface of the composite vein is called "epipleuron" by analogy to the
corresponding structure in beetles. In the studied material Pc was the longest in *Otiocerus*
reaching 80—90 % of the length of the costal margin and the shortest in *Delhina* (Figs. 9,
172) where it curves mesad and fades at the level of the "basal cell". In numerous Issidae

Pc is slightly extending ventrad at the very base (Fig. 173) becoming the ventral termination of the very broad complex vein containing a large common lumen. The Pc becomes strongly shifted mesad making the epipleuron inclined ventro-mesad (Fig. 174) or if there is an accompanying curvature of the corial part of the wing, the surface of the epipleuron becomes parallel to the substratum. In most of the Fulgoroidea Pc is quite low and forms only the lowest part of the epipleuron. The presence of a demarcation line in this region is rather exceptional and was observed in some Achilidae and in *Pelitropis rotulata* (Fig. 176). Praecosta being primarily an anterior marginal vein, in most of groups tends to be ventral and at its mesal proximity becomes associated with the usually slightly depressed CP. In families Flatidae, Nogodinidae, Lophopidae, Ricaniidae, Eurybrachyidae, Tropiduchidae with a few exceptions, in some Fulgoridae and in *?Ateson consimile* (Achilidae) Pc is strongly associated with CP only, from its very base being shifted mesad from CA which in these cases alone forms the costal margin. Components of this composite vein (Pc+CP) retain their association with the band of sclerites of articulation (Fig. 8) and are identifiable owing to their landmarks (Fig. 175).

Costa Anterior (CA)

In all examined cases this vein forms the next (after Pc) detectable extension on the dorsal (Fig. 3), latero-dorsal (Fig. 4), or the very lateral margin of the fore wing (Fig. 6). In the wings with Pc+CP vein, CA containing distinct separate haemolymph channel retains a connection with CP through a system of perpendicular veinlets or through a narrow lacuna if the distance between both veins is very small. In *Neotylana* (Fig. 10) CA forms at its very base an extraordinary ear-like lobe protruding dorso-mesad over the wing surface with its concavity, made by the ventral surface of the wing, directed forward. The margins of the lobe (CA itself) are lined with two kinds of highly differentiated and well innervated sensillae arranged in two regular rows. The whole structure seems to act analogously as a radar dish what would be quite unique function of CA. In all Fulgoroidea further out, CA gradually loses its separate identity and finally passes into the marginal blade or marginal membrane. If CA has a separate channel, the channel joins channels of subsequent veins and together they form the ambient vein (av), sensillae of CA become lost or associated with the ambient vein too.

Costa Posterior (CP)

This vein in all studied species remains the most stable component of the costal complex but never exists separately at the base of wing. Costa Posterior is the only vein of the three that contains beside the haemolymph channel also costal nerve and costal trachea. All sensillae associated with Pc or CA are innervated by the costal nerve and the same applies to the tracheation. Thus the costal nerve and the costal trachea are the landmarks for CP. The vein is usually seen as a mild depression immediately mesad of the elevated ridge of CA on the dorsal side. In most of the Fulgoroidea it forms a composite vein together with Pc and CA being hardly demarcated from CA. However in the above mentioned groups as e. g. Flatidae it separates from CA, associates with Pc (which in these groups in ventral) forming mesally the very base of the composite vein Pc+CP (above Pc) (Fig. 175) and remains identifiable owing to its landmarks: nerve and trachea. In some Issidae CP leaves the primarily more marginal veins Pc and CA, regardless their relationship to each other, and undertakes the course mesad (Figs. 11, 12, 19, 171, 174). In the groups with the composite vein Pc+CP, Pc becomes indistinguishable more terminally and then CP approximates to ScP, always forming a depressed area in this region. The area is also more weakly sclerotized and facilitates flexion downward being the costal end of the homologue of the nodal line of cicadas. In Cixiidae, Achilidae and some others the approximation of CP and ScP is even closer (Figs. 39, 66, 68, 74, 79) and also is connected with the costal end of the nodal line immediately behind, finally they merge into the ambient vein.
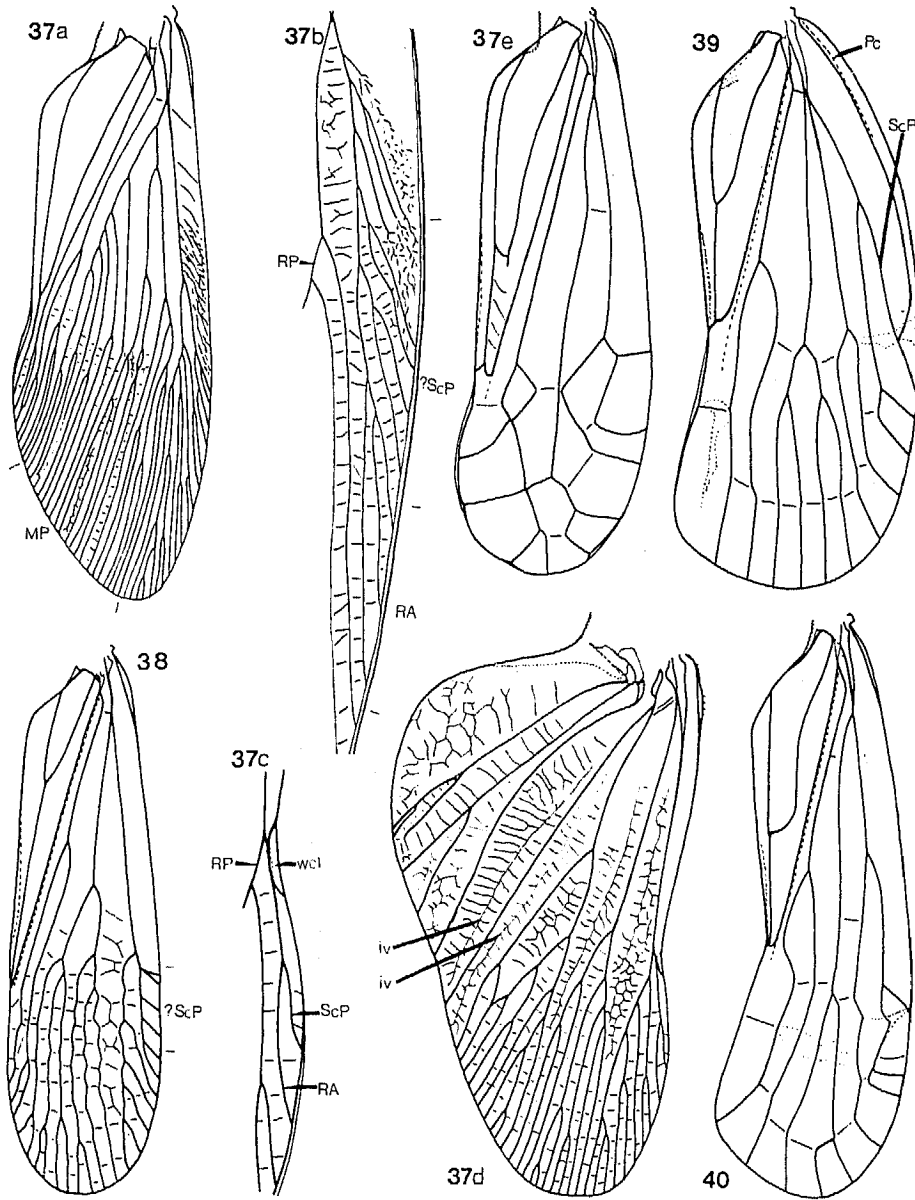
Figs. 37a—e, 38—40.
Enchophora: 37a—d. — 37b: Sc-RA region of the other fore wing in higher magnification — 37c: region of the wcl in higher magnification — *Ipsnola*: 37e — *Dictyophara*: 38 — Achilidae g. sp. (S. Africa), areas closed by dotted lines mark less sclerotized parts of membrane contributing to the nodal line: 39, 40.

C i c a d o i d e a . Praecosta (Pc)
In all studied species including the genus *Tettigarcta*, Pc is situated at the wing edge forming a rounded margin. In most species of singing cicadas [2]) the distance between Pc and

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[2]) The vernacular name is retained here to refer separately to Cicadoidea other than *Tettigarcta*.
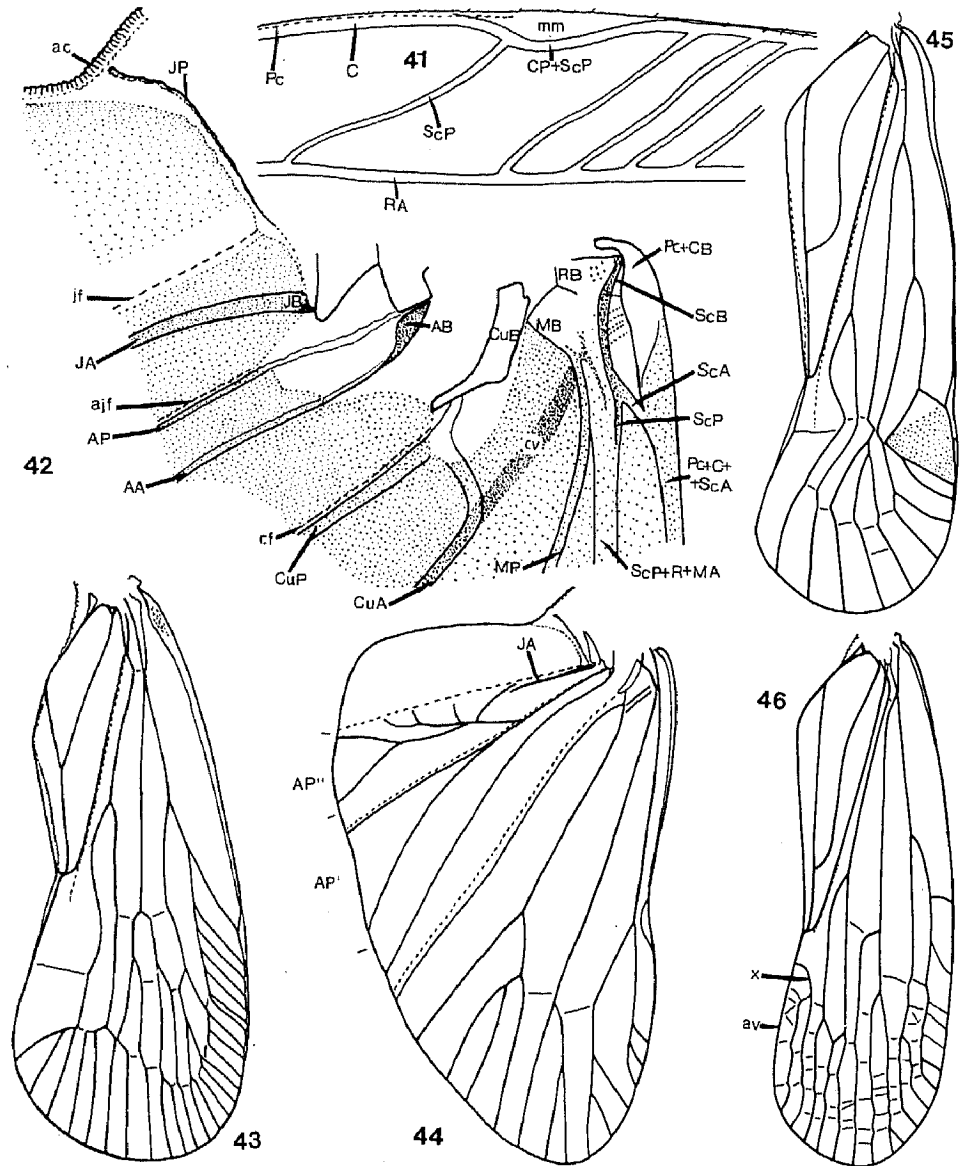
Figs. 41—46.
? *Elidiptera:* 41—44. 41: region of the costal nodus in higher magnification, costal margin turned up, Pc marked by interrupted lines — 42: base of the hind wing (MA marked by dotted pattern as a sclerotization superimposed on R basally) — ? *Koloptera* (from Equador): 45 — *Rhotala* (the accessory vein, labeled x, contains anal trachea): 46.

the next vein is unconspicuous, in some others a noticeable space is observable subbasally at the curve of the wing margin (Fig. 92) but even then the haemolymph channel is common to all veins of the costal complex (Fig. 91). In *Tettigarcta* the distance between Pc and C is more uniform up to the nodal line. Pc is heavily sclerotized on both sides, it fades away at the nodal line.
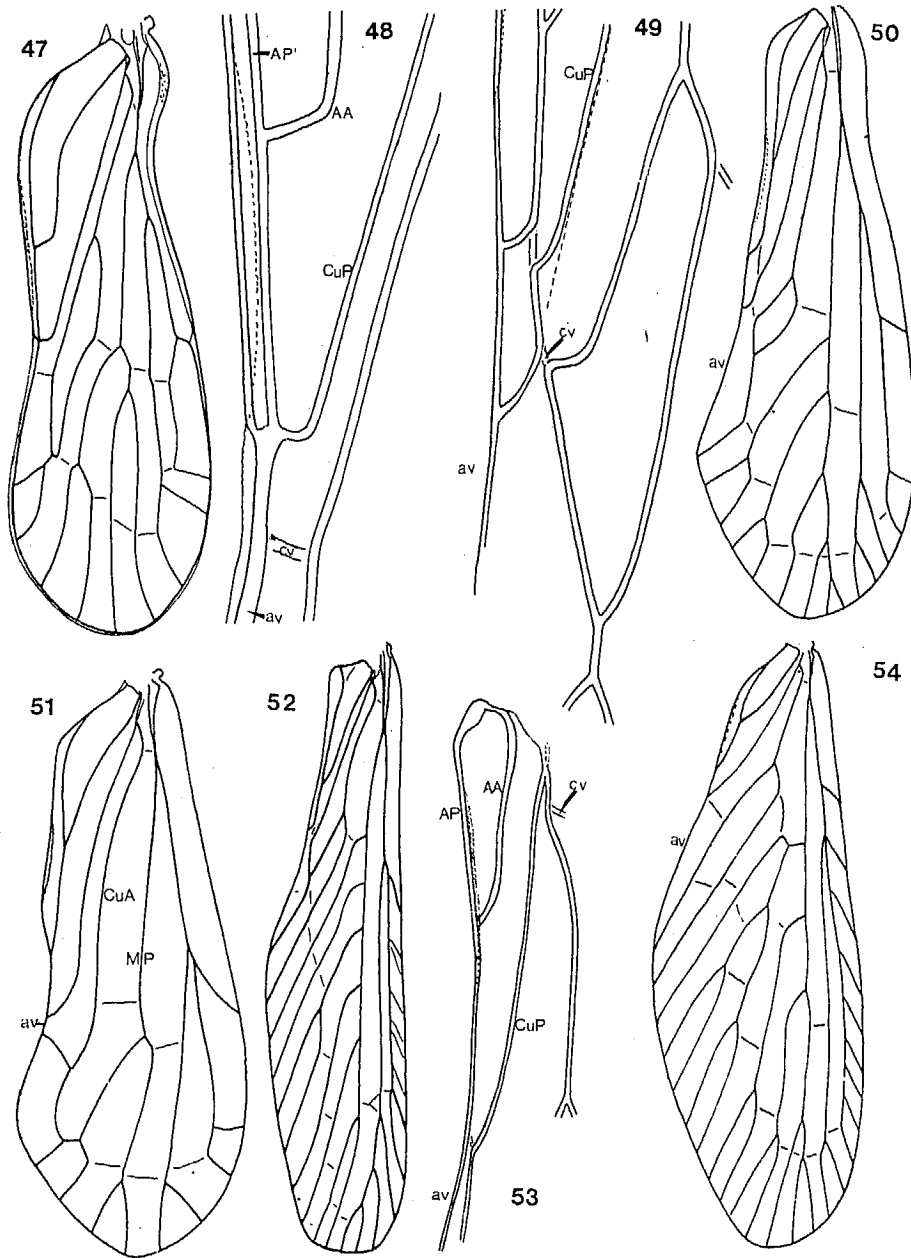
Figs. 47—54.
Achilixius: 47, 48. 48: region of the tip of clavus (claval nodus) in higher magnification —
Anotia: 49, 50 (two different species) — *Patara*: 51 — Derbidae g. sp. (S. Africa): 52 —
Muiria, region of clavus: 53 — *Mysidia*: 54.

Costa Anterior (CA) and Costa Posterior (CP)

In singing cicadas this is the most prominent vein of the fore wing being strongly convex
on the dorsal side and several times more voluminous than Pc (Fig. 91). It contains
trachea and nerve and continues beyond the nodal line joining twice with re-emerging ScP

(Figs. 94, 97). In some cases the curvature of the costal wall is very similar to the typical epipleuron of Fulgoroidea if the last would have been spread horizontally. In *Tettigarcta* CA+CP is less prominent and there is the large area separating the pronating unit from the following veins (Fig. 95) while in singing cicadas the space is often almost nonexistant. Relation of C to ScP subterminally is the same in all Cicadoidea.

Cercopoidea. Praecosta (Pc)

The fore wing is strongly sclerotized and veins are often hardly identifiable without reference to the nerves or tracheae. Especially it is true regarding veins of the costal complex in which certain veins can be distinguished only in parts of their distinct elevation. In all species that were examined Pc does not reach much further than the double length of the cubital triangle. In most Aphrophoridae Pc forms a marginal ledge at least basally tapering ventrad (Figs. 117, 125, 129) comparable to the same of *Hysteropterum* (Issidae) or *Oliarus* (Cixiidae) (Fig. 4). In others Pc is shifted mesad on the ventral side of the wing running more or less parallel to the costal margin (Figs. 115, 116, 118) or arcuately curving mesad toward ScP (Fig. 119). In the all wings Pc forms heavily sclerotized usually high ventral extension provided with the scaly sculpture on the site corresponding to that in Fulgoroidea. Veins of the costal complex are sculptured also beyond base but the scales never show the direction that is characteristic for Pc. In Cercopidae Pc is inclined mesad, forming near base the epipleuron closely resembling that of *Colmadona testudinaria* (Issidae). In all examined species Pc was fused with other elements of the costal complex basally but showing a separate connection with the "humeral plate" on the ventral side (Fig. 120).

Costa Anterior (CA) and Costa Posterior (CP)

Both costal veins occupy marginal position when viewed from the dorsal side because Pc is always ventral or bent ventrad. The CA and CP can not be identified otherwise than in accordance to the route of the costal nerve and the costal trachea which by comparison with Fulgoroidea are expected to be associated with CP. The marginal extension, if present, could be identified as CA similarly as in Issidae with Pc strongly shilfted mesad. The costal veins occupy quite large space judging after position of the trachea and the nerve. Usually there is no easily distinguishable point where both costal veins pass into the ambient vein (Figs. 121, 124). At the very base CP borders on a sclerotized streak, neutral in fluting, behind which is the postcostal flexion line (Fig. 120) as in Fulgoroidea.

Cicadelloidea. Praecosta (Pc), Costa Anterior (CA) and Costa Posterior (CP)

In all cases the three veins are completely fused together. Pc can be recognized owing to its characteristic reversed scaly sculpture (Fig. 143) and further by the ledge on the epipleuron most probably demarcating border between it and C (Figs. 141–144, 146, 147). The epipleuron is often strongly shifted lateral and in the dorsal view visible before C when the wing is pressed in slide, but in the natural position Pc is a much more ventral vein. In some species the composite vein is almost rounded in cross-section and the terminal end of Pc is not distinct. CA is identifiable as a high ridge on the dorsal side, sometimes even inclined mesad (Fig. 141). CP is identifiable only by the position of the nerve and the trachea analogous in Cercopoidea. Also as in Cercopoidea, separate bases of Pc and costal veins are detectable. The basal attachment of the veins of the costal complex can be difficult to trace because of desclerotization and depigmentation in this region. The composite marginal vein is usually richly sculptured but in most of the examples under study the characteristic Pc sculpture on a small area restricted to the subbasal region is easily observable. Similarly to Cercopoidea there is a distinct sclerotized streak — a rod belonging to CP, running for a short distance in front of the post-costal flexion line (Fig. 140).
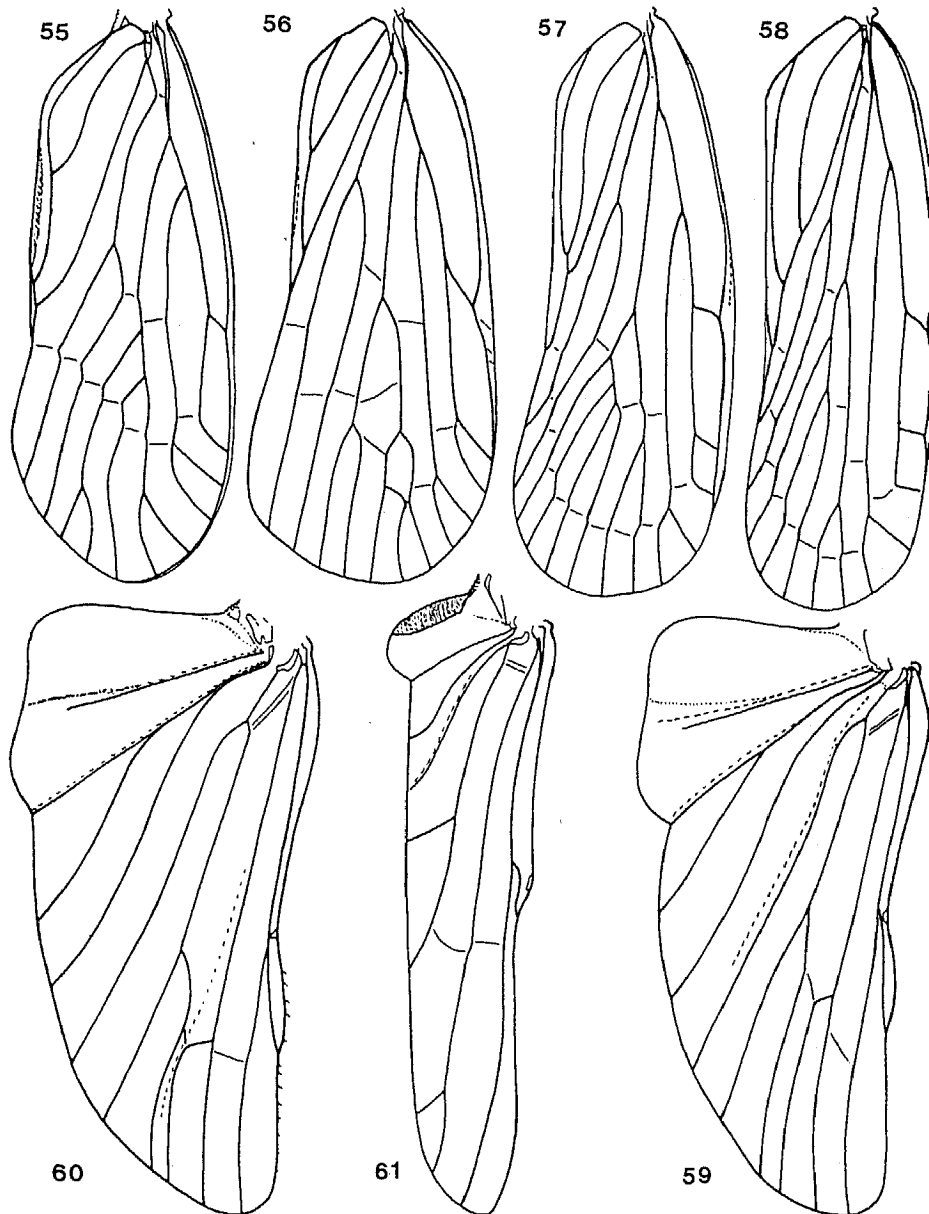
Figs. 55—61.
Cedusa: 55 (from Mexico), 56 (from Equador) — *Herpis* (end of Pc marked by interrupted lines): 57 — *Persis (Anapersis)*: 58, 59 — *Omolicna*: 60 — Derbidae g. sp. (S. Africa): 61. In Figs. 59 and 60th haemolymph channel in the jugal lobe declines mesad of the jugal fold.

## Hind wing

Fulgoroidea. Praecosta (Pc)

In *Ricania fenestrata* this vein has a separate identity subbasally (Fig. 25) being slightly inclined downward and only slightly elevated to compare to the next vein. It does not bear sensillae but it is richly ornamented with small cuticular teeth (Fig. 26). After the
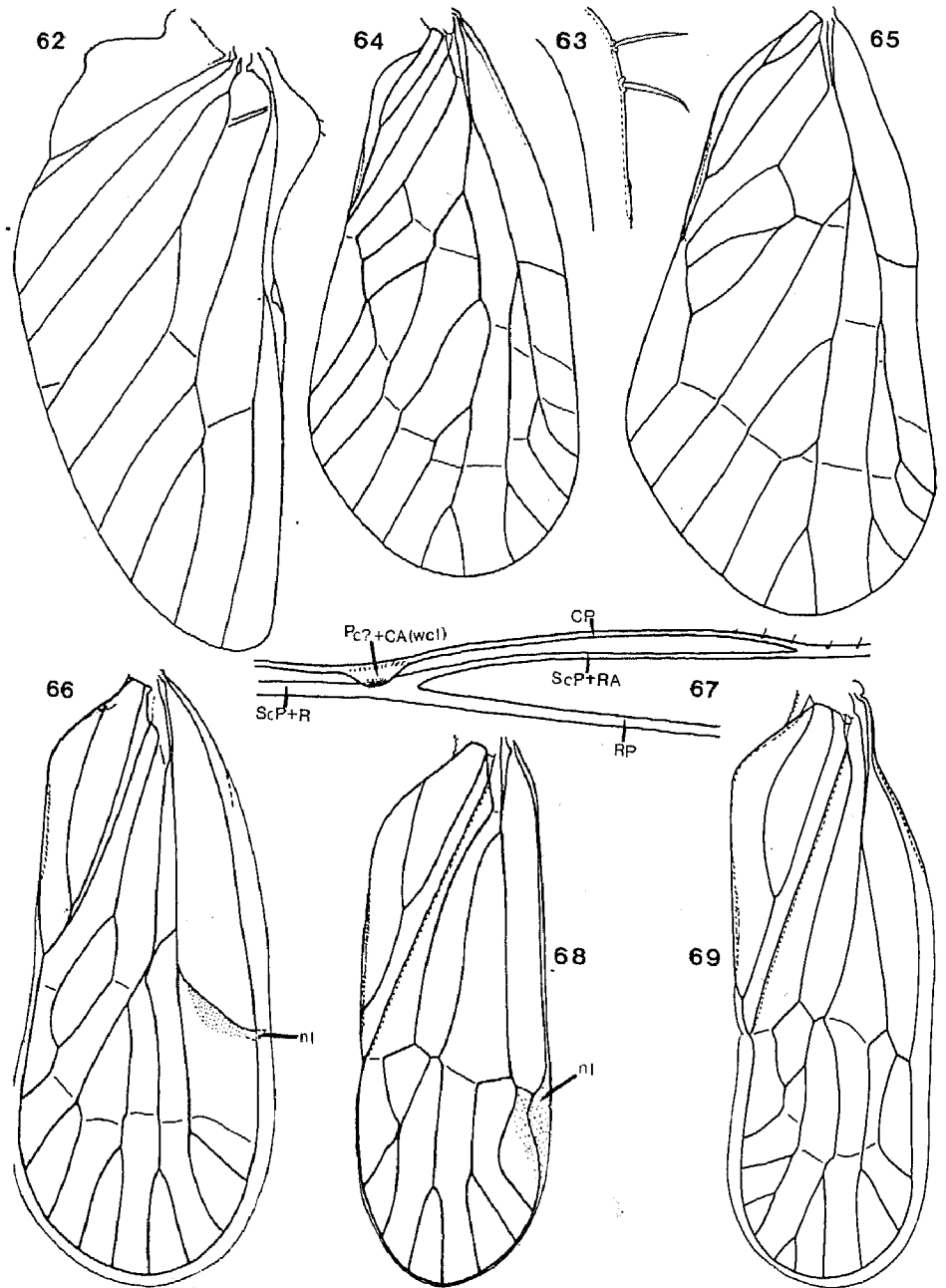
Figs. 62—69.
Mysidia, hind wing (JA attached to AP): 62 — 63: sensillae on the composite marginal vein
— *Leou*: 64 — *Saccharodite*: 65 — *Kinnara ? fumata* (MEL.): 66 — *Neocenchrea*: 67, region
of the wcl, the costal margin turned up — *Eparmenoides*: 68 — *Anigrus sordidus* STÅL: 69.

expansion of the wing margin it turns dorsad over the next vein fusing with it but its
cuticular sculpture remains detectable consisting of numerous cuticular teeth that are
smaller than these on CA (Fig. 27). Finally Pc broadens into a lobe that is bent up mesad
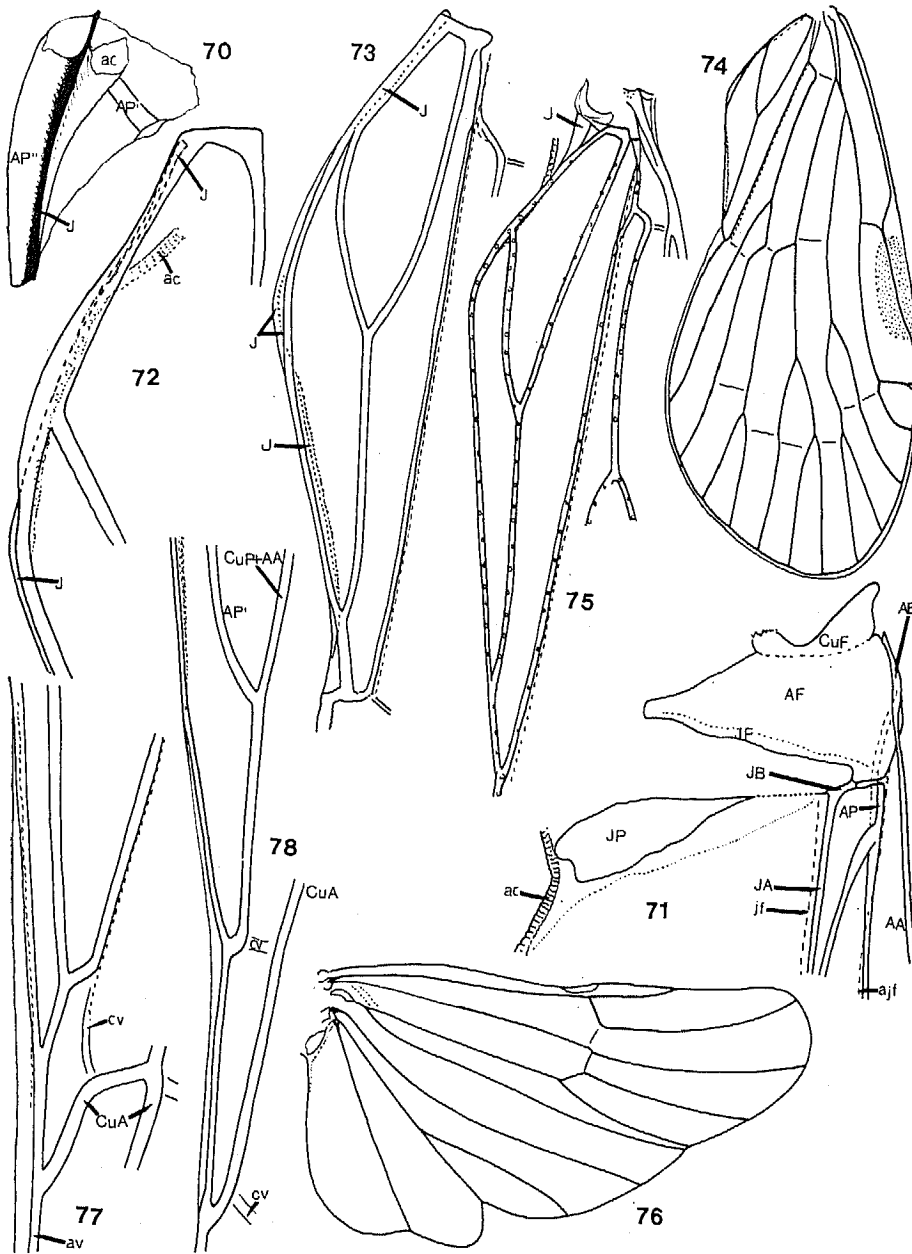
Figs. 70—78.
Oliarus, region of AP—J with emerging axillary cord, ventral side (half schematic): 70 —
Oliarus, basal region of ano-jugal complex ("Ax3" contains Cu-J Fulcralaria, the two folds
at both sides of JP omitted from the drawing for the sake of clarity, the more basal one
in most of wings cuts off JB from JF): 71 — *Numicia*, proximal and inner parts of clavus,
dorsal view: 72 — *Bothriocera*: 73, 74 — Cixiidae g. sp.: 75, 76 — *Ricania fenestrata* (F.),
tip of clavus (total wing in Fig. 24): 77 — *Persis (Anapersis)* (total wing in Fig. 58): 78.

extending over C and over a part of the costal cell (Fig. 28). This is the wing coupling
lobe (wcl) (OSSIANNILSSON, 1950) and Pc terminates on it acquiring additional sculpture
and prolonged curvature that facilitates coupling with the fore wing during flight. In

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Entomol. Abh. Mus. Tierkd. Dresden 52, Nr. 3 (1988)

other groups Pc is completely fused with C and separated only terminaly (Fig. 14) but in many Eurybrachyidae, Fulgoridae and Achilidae there is a double corrugation on the composite marginal vein and the more ventral ledge (near the base) very likely represents Pc. In some other species it is also easy to trace the change of the position of Pc from basally ventral to anterior and finally to dorsal, terminating on the wcl. In *Enchophora* (Fulgoridae), *Otiocerus* (Derbidae), *Bothriocera* (Cixiidae) and *Varcia* (Nogodinidae) there is the continuous row of cuticular teeth marking the patch of Pc.

Costa Anterior (CA) and Costa Posterior (CP)

Both veins are always fused together (usually also with Pc). CA is dorsal and sometimes shows considerable elevation e. g. in *Ricania fenestrata*. CA+CP continues after wcl, then fuses with re-emerged ScP or ScP+RA and merges into the av. Usually av is marginal at the costal margin and before the fusion it is hard to detect any sign of CA on the very margin. CA+CP contains trachea and nerve which serves a few, sometimes big (e. g. in Flatidae) sensory setae situated on the more or less expanded wing margin subbasally (Figs. 34, 62, 63). More numerous and smaller, also innervated, setae are grouped basally and some others even at the beginning of av. Basal articulation is obscure owing to crowding of the veins near costal margin.

Cicadoidea. Praecosta (Pc)

This vein is always fused to both costal veins, marked only at base by rich sculpture, then undistinguishable until wcl. In singing cicadas the wcl maintains a narrow lumen common with costal veins (Fig. 104) for they join ScP+RA there (Fig. 113). In the presented cross--section it is visible that a small part of presumably CA participates in forming the wcl. In *Tettigarcta* Pc emerging terminally to form the wcl has a minute lumen of its own at the margin and ScP+RA takes the haemolymph volume from the composite costal vein before wcl (Fig. 112).

### Costa Anterior (CA) and Costa Posterior (CP)

These veins always fuse together (also with Pc), contain nerve and trachea and in singing cicadas bear numerous setae corresponding to the similarly situated setae on the costal margin in Fulgoroidea. Usually Pc+C is richly ornamented with variously shaped scaly sculpture. In singing cicadas at the end or just after the wcl ScP joins the costal veins (sometimes only as an obscure lacuna) and after that the composite vein CP+ScP turns mesad to join RA forming an arch (Fig. 113). The minute lumen and a remnant of sculpture at the border of marginal membrane can be ascribed to fading CA. In *Tettigarcta* there is a conspicuous incision of the outline of wing at the costal margin and at the proximal end of this incision a quite peculiar structure, apparently associated with C can be found (Figs. 108—110). This consists of a considerably long dorso-posteriorly curved stump terminated on a peg. In *T. tomentosa* there was observed one larger and one somewhat reduced such "hook" while in *T. ?crinita* there were two big ones. The true nature of this structure could not be established for the very limited access to the material but it resembles very much the "hamuli" of Cercopoidea.

Cercopoidea. Praecosta (Pc)

The Pc is fused to both costal veins completely and only by comparison with Fulgoroidea it is possible to distinguish it terminally as the wcl (Fig. 132).

### Costa Anterior (CA) and Costa Posterior (CP)

The both veins are always fused together and with Pc and are quite narrow, however the haemolymph must flow through lacuna into ScP+RA behind the wcl for there was found
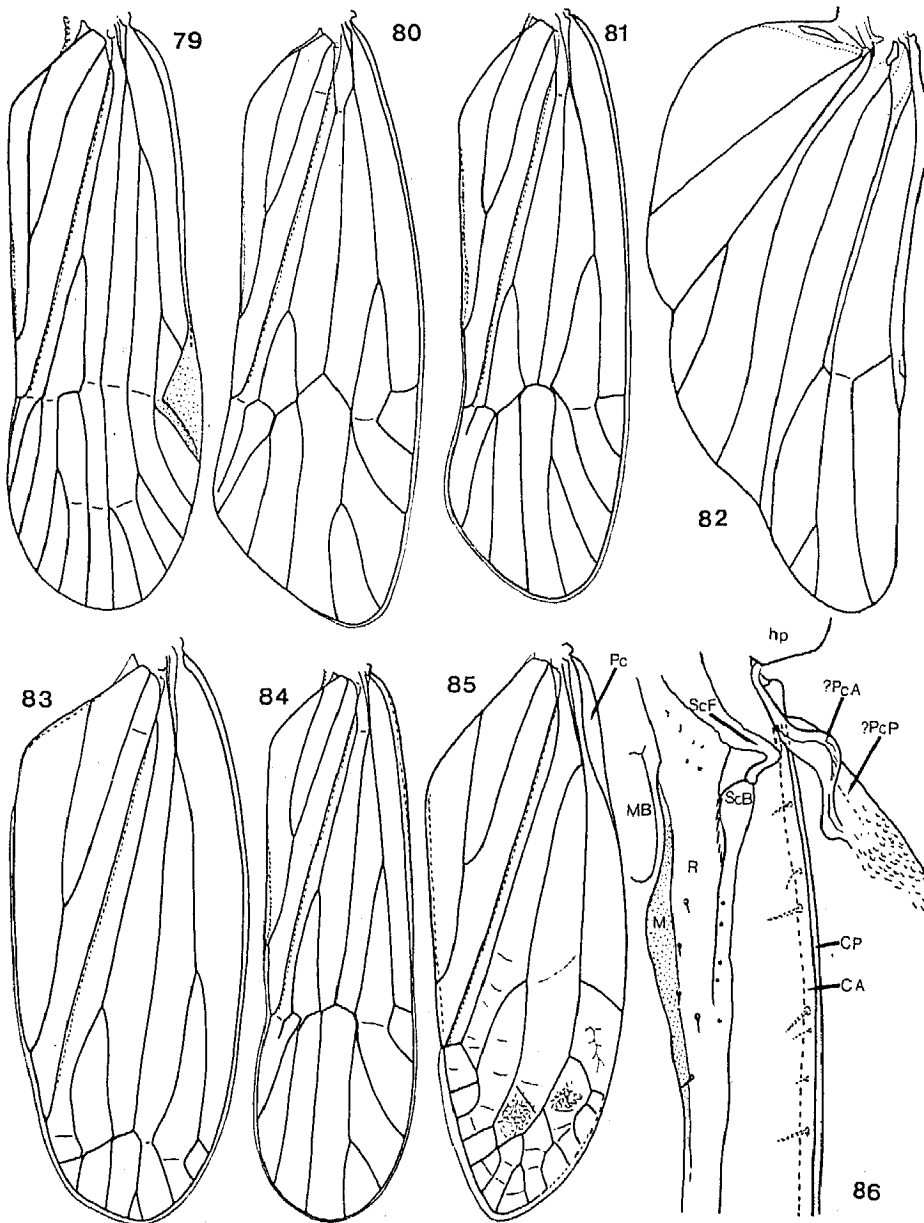
Figs. 79—86.
Ugyops ? taraculae (MUIR): 79 — Delphacidae g. sp.: 80—84 (80 from S. Africa, others from Equador) — *Tettigometra ?sulphurea* M. R. (basal part of the costal complex of *Hilda patruelis* [STÅL]: 85 — *Hilda patruelis* (STÅL), basal attachment of Pc—M veins, ventral side (CA misplaced in the slide): 86.

no veinal connection between the costal complex and the following veins terminally, except of a rudiment of the av in some Cercopidae (Fig. 126) and a ?cross-vein in *Ptyelus*. The wing margin broadens subbasally into a large bent up lobe which bears a few enlarged, often peg-like sensillae (Figs. 129—131) sometimes situated on well protruding lobate stems

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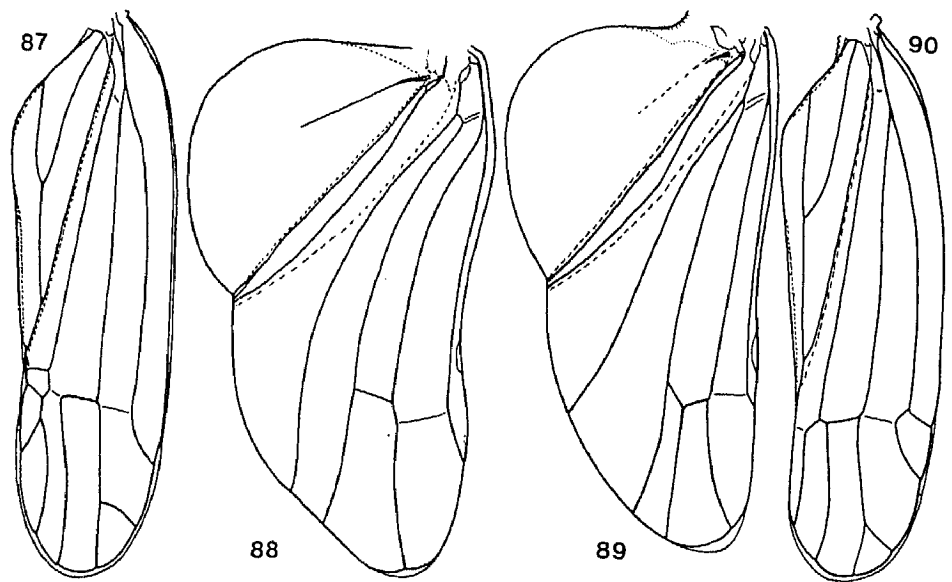
Figs. 87—90.
Peltonotellus nigroviridia (BALL): 87, 88 — *P. histrionicus* STÅL: 89—90.

arising from C. These setae called "hamuli" (EMELJANOV, 1977) as well as minute setae more basally, correspond to the similar ones in other superfamilies.

Cicadelloidea. Praecosta (Pc), Costa Anterior (CA) and Costa Posterior (CP)

The three veins are fused together forming quite strong marginal vein on which the wcl can be identified as terminal part of Pc. Often the vein is covered with rich scaly sculpture. Behind the wcl remnants of the sculpture remain at the border of the marginal membrane marking the fading CA, and a well defined vein that can be identified as CP turns mesad and joins ScP+RA, becoming further on the av (Fig. 159). In some Cicadellini (Figs. 162, 164), in subfamily Typhlocybinae and in some others there are reductions in this region resembling these of Cercopoidea (Fig. 163). In some cases the veins of the costal complex remain at the margin for a short distance behind the wcl and ScP+RA joins them and then the complex vein fades and the haemolymph is dispersed (Fig. 161). This arrangement exactly corresponds to that found in Fulgoroidea where the av occupies the very margin of the wing not leaving any free membrane anteriorly (Fig. 67). The only difference is that in these Cicadelloidea the av is reduced and this makes impression of presence of a large marginal membrane (Fig. 162). Basally on the composite vein there is a group of small setae and on the slightly produced curvature subbasally a row of larger sensory setae as in other superfamilies (Fig. 156) but short and sometimes of a very peculiar shape (Figs. 157, 158).

Discussion of the pronating unit — costal complex

The veins of the costal complex were more often subject to misinterpretation than any other veinal unit. The reason for this were: neglecting the connection with the sclerites of the dorsal articulation, overestimating the meaning of basal tracheation of larval wing pads, and basing the study on too limited material. Because of that the pronating unit could not be clearly separated from the next one and the atracheate veins Pc and CA were overlooked. Also the spatial relation between veins in wings with "praecostal field" was poorly examined except by FENNAH (1944). The separate identity of Pc was not noticed or it
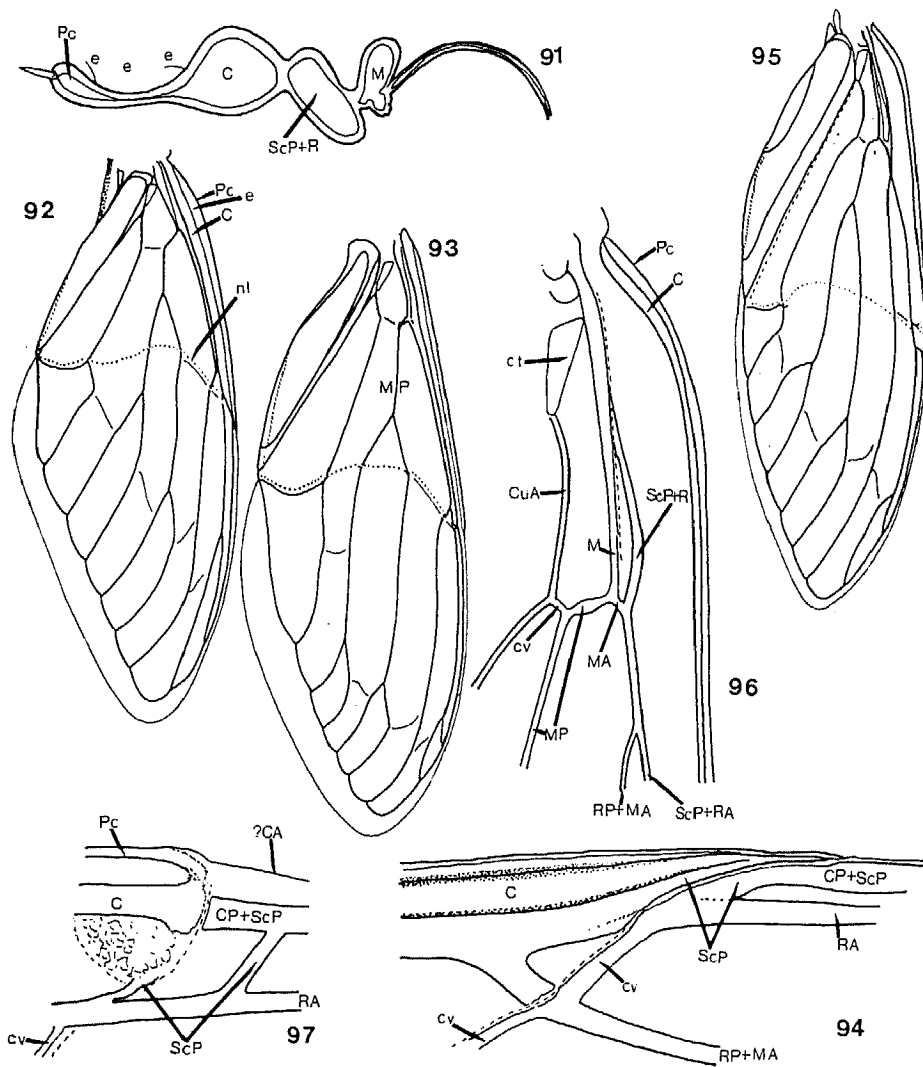
Figs. 91–97.

Platypleura divisa (GERM.): 91, 92. 91: transverse cross-section through the costal part of the fore wing at the level of the end of cubital triangle, the membrane to the right belongs to the "basal cell" — 92: fore wing, the nodal line dotted — *Chonosia*: 93, 94. 94: region of the costal nodus in higher magnification, the costal margin turned up — *Tettigarcta tomentosa* WHITE: 95–97 (96 and 97 free hand drawings).

was regarded as a keel on costa or as costa when the CA was regarded as a keel (both in: EMELJANOV, 1977). FENNAH (1944) stated that "there is no trace of praecostal vein in ... Fulgoroidea ... nor ... such a vein ... have been detected in any fossil ascribable to this superfamily". But it was FENNAH who recognized the EMELJANOV's "basal anterior keel" as the true costal margin although Pc and CP are undiscriminated in his diagram (Fig. 1). In the present study Pc as a distinct separate vein is found as the marginal vein up to the nodal line (nl) in the fore wing of Cicadoidea (Figs. 91, 92, 97) and in the sub-basal part of the costal margin of the hind wing of Ricaniidae (Fig. 25). This identification is based on the 1st and 3rd major criteria of homology. Very similar picture as for Rica-

niidae has been presented for Prosbolidae e. g. *Prosbole ivagorae* BECK.-MIG. and *P. brevi-alata* BECK.-MIG. (p. 199 in: EVANS, 1956) from Permian of Russia. True, Prosbolidae are not Fulgoroidea (SHCHERBAKOV, 1984) but the presence of free Pc in Ricaniidae is evident. Also the separate anterior free ledge in the fore wing of Tettigometridae bearing Pc landmark (the 1st and 2nd major criteria of homology), epipleuron with demarcating line between Pc and CA (Figs. 141, 146, 147, 176) and prominent to a various degree the lower keel terminating the marginal composite vein in the fore wing of most of Fulgoroidea support my interpretation of this vein (the 3rd major criterium of homology). The best examples of the intermediate conditions of Pc show wings of many Issidae (Figs. 172—175) as well as Cercopoidea (Figs. 116—119), in *Clastoptera* and *Delhina* Pc is inclined mesad terminally while CP is still approximated to CA. EMELJANOV (1977) described the composite costal vein in the way I find too obscure to comment. Instead, I am translating the two passages presenting his views: op. cit. p. 25 "The costal vein of [Dictyopharidae, Fulgoridae] and many other Fulgoroidea forms at the base of [the fore] wing an anterior keel and an upper one which gradually passes anterial in the midlength of the costal margin, and more apically appears before the basal anterior keel. The costal trachea, as shown by FENNAH (1944), follows the basal anterior keel, which he even recognizes as the true costal margin. Such a point of view is quite scholastic and in this case rather inaccurate, because in many other families of Fulgoroidea, in which the praecostal field is present, the upper keel becomes the anterior one on the whole length of costal margin and the anterior one simply forms the lower wall of the true costal vein. In primitive Cixiidae — *Andes* and others, the so-called upper keel is developed as the anterior one on the whole length. It is more likely that the keel, being the anterior one terminally, turns dorsad at the base of the wing." Same, pp. 18 and 19 "In the fore wing of Fulgoroidea the costa most frequently is situated marginally (submarginally) continuing up to join the first branch of subcosta. Sometimes the praecostal field is developed that corresponds to the expansion of the truly anterior crista of the costal vein. In Fulgoroidea without the praecostal field and also in Cercopoidea and Cicadelloidea this anterior crista in the basal part of the anterior margin of the fore wing turns dorsad, and the lower crista on the costa seems to be the real costal margin. More terminally the anterior crista of costa returns to its initial position, so does the lower crista, except that the upper keel appears. The upper and lower keels are distinctly protruding walls of the costal vein and the anterior keel [is a] marginal membrane, however in the basal part of the wing the keels look differently [rather] like cristae. Where the praecostal field is present the lower keel appears far from the wing margin but does not change its position in relation to the costal vein. In some Issidae the lower keel forms a false praecostal field [? as in Fig. 174]. As was shown by FENNAH (1944) the marginal vein of the praecostal field is false (primarily) atracheate." The lack of clarity in the above texts is evident and that is the best proof that the problem was not easy to solve. EMELJANOV's idea about keels on Costa is applied to the Permian Cicadomorpha by SHCHERBAKOV (1984). He writes that the upper and lower keels are small there and the anterior one is inclined upwards and forms a welt on the dorsal side of the fore wing. This "welt" is angulately broadened subbasally and from the angle the short ventral keel arises. This short ventral structure is labeled CP that could mean Costa Posterior, but there is no such statement in the text. If the reconstruction is correct, the ventral keel must be a vein because otherwise there would be no explanation for the affecting the shape of the dorsal "welt" by the ventrally extending keel (or vice versa).

The interpretation of such veins as Pc and CA as keels on one vein (one can see from the above citations that it is easy to get lost following the idea) is in disaccordance with observable facts. For how to explain that just a keel (a structure commonly occurring on many parts of body of Fulgoroidea and known as a labile character) remains so conservatively in all superfamilies of Auchenorrhyncha, in most of them retaining a distinct landmark? Also, if it would be only an extension on some other vein it must always retain the attachment to this vein and do not occupy an independent position (e. g. Pc in *Clastoptera*
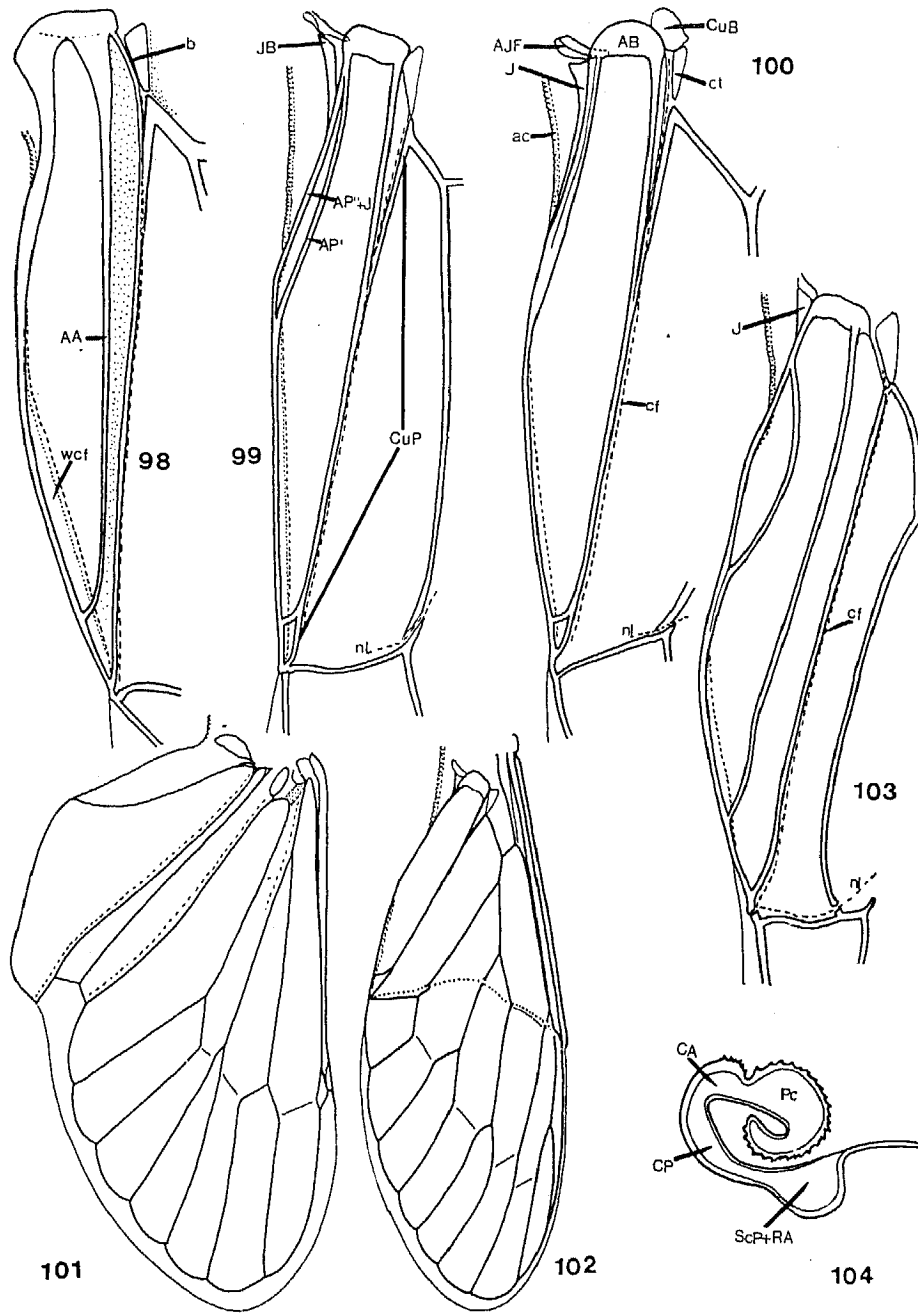
Figs. 98—104.
Chonosia, clavus and adjacent parts of the wing, the brace is formed here by ? AA′ (total wing in Fig. 93): 98 — cicada from Panama: 99 — *Melampsalta*: 100—102 — *Tettigarcta tomentosa* WHITE (total wing in Fig. 95): 103 — *Magicicada septendecim* (L.), transverse cross-section through centre of the wcl (after OSSIANNILSSON, 1950, explanations added): 104.

and *Delhina*, fore wing of Cicadoidea, hind wing of Ricaniidae). It would be truly ridiculous that processus xiphoideus of the mammal sternum in one group of animals leaves its traditional attachment and moves to another bone! Other evidences that Pc and CA, in my interpretation, can not be merely cuticular extensions on the costal vein is that both of them when separated (Pc in fore wing of Cicadoidea and in hind wing of Ricaniidae, CA in the fore wing of insects with Pc+CP composite vein) maintain their own haemolymph channels, all have basal connection and their spatial arrangement viewed from the costal margin is comparable including the cases where there is Pc+CP vein. The changes of the position among veins of the pronating unit are the most spectacular in wings with Pc+CP vein and ca cell ("praecostal area" of authors) e. g. Flatidae. The possibility that the vein behind "praecostal area" is Sc (MUIR, 1923 in: FENNAH, 1944: CHOU et al., 1985) must be ruled out because in Fig. 175 it is clearly visible that the veins in question belong to the pronating unit while ScP is fused to R. The best graphical explanation of how the composite ventral vein Pc+CP originates was given by FENNAH (1944). This representation (Fig. 1) is based on the wing of *Fulgora* but the distinguished parts of the scheme are correctly homologized with quite dissimilar costal complex veins of *Mnemosyne* (Cixiidae) and compared with a few Tropiduchidae showing the intermediate conditions. I suppose that all the above sufficiently explained the real nature of the vein behind "praecostal field". The only question remains whether Pc moved ventrad or Ca shifted laterad? In the scheme of the flying wing (KUKALOVA-PECK, 1983, Fig. 15) Pc is primarily the marginal vein as it is in Cicadoidea and Tettigometridae. When to compare the shape of Pc in insects where it occupies various positions it appears that the difference is made by the overgrowth of CA. Therefore the expansion of CA is the cause and the connection of CP with Pc must follow. Another reason for that interpretation is discussed elsewhere. *Ricania fenestrata* and maybe all Ricaniidae are exceptions devoid of the scaly sculpture being the landmark of Pc. But if to refer to the costal trachea as the landmark of CP, the CP goes parallel to the anterior margin (CA) at its start, subsequently turns mesad in a form of an arch and only finally joins the straight solid vein which after this point becomes the composite vein. Thus it follows that the solid straight vein at the very base can not be anything else but Pc.

The costal vein understood as a single one and found as identical with the first branch of bifurcating first anterior trachea of larval wing pad was recognized as marginal or submarginal (in insects with Pc+CP vein) in the fore wing of Fulgoroidea by METCALF (1913b) that was repeated by FENNAH (1944), EMELJANOV (1977) and SHOHERBAKOV (1981). Basing on the scheme of larval tracheation of Fulgoroidea and preoccupied by the sequence of the tracheae METCALF (1913a) stated "costa practically disappeared from Jassidae" for the utmost anterior trachea of the wing pad was single in most of studied examples. The inconspicuous branch in front of it, found only in *Gypona*, has been interpreted as costal trachea (and also costal vein) which disappears in adults. The bigger trachea, the most often the only one in larval wing pad of Cicadelloidea, was by sequence the second and only because of that it was called the subcostal trachea. The minute branch in front of the bigger trachea at the costal margin was found also in many Membracidae (FUNKHOUSER, 1913) (Fig. 139). Thus the identical reasoning led both METCALF (1913a) and FUNKHOUSER (1913) to the recognition of the marginal composite vein of Cicadelloidea as Subcosta and was repeated by many others. However, if to use the 1st major criterium of homology the both tracheae parallel to the costal margin (Fig. 139) in Cicadelloidea can be recognized as belonging to the veins of the costal complex. The weak anterior tracheal branch might belong to Pc or rather to CA because CA is the next vein and in other cases it receives more containment from CP than Pc. Moreover, except in Cicadelloidea, this little anterior trachea is also found in *Thionia* (Issidae) (METCALF, 1913b, Fig. 27) having complete "costal" and "subcostal" tracheae of the authors. FUNKHOUSER (1913) suggests that the strip of membrane in front of the veins in the fore wing of Membracidae might be the atracheate Costa (in my interpretation it is atracheate in
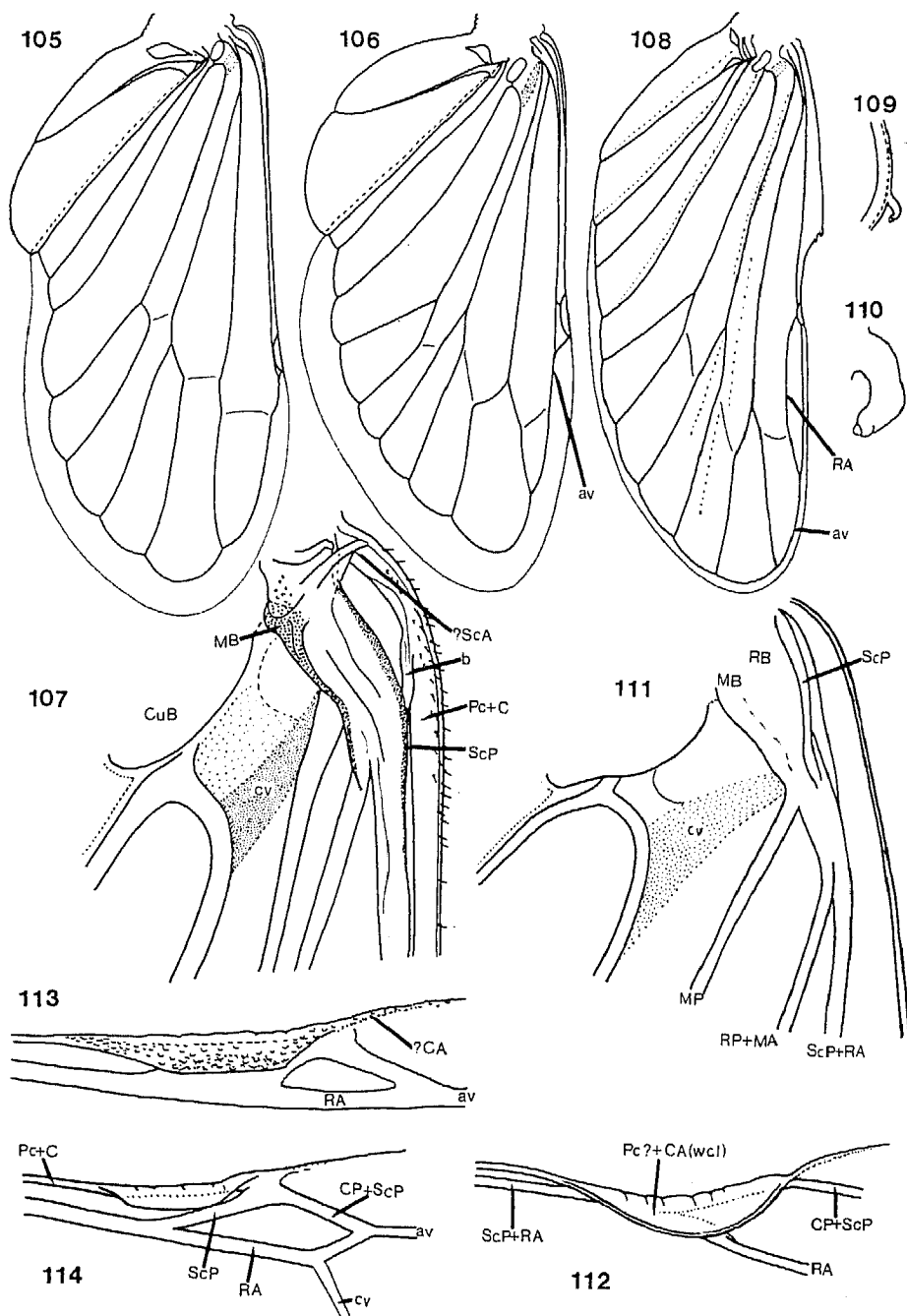
Figs. 105—114.

Calopsaltria longula (STÅL): 105 — *Okanagana*: 106, 107. 107: basal attachment of veins up to Cu in the hind wing, dorsal view (the brace here is formed by CP or ScA) — *Tettigarcta tomentosa* WHITE: 108—112. 109: situation of the marginal "peg" on Pc+C — 110: "peg" in higher magnification — 111: basal attachment of veins up to Cu in the hind wing, ventral view — 112: region of wcl, the costal margin turned up (109—112: free hand drawings) — ? *Taipinga*: 113 — *Melampsalta* (total wing in Fig. 101): 114.

adults CA or parts of CA). EMELJANOV (1977) has interpreted these two tracheae as "a way of development of imaginal trachea at nymphal trachea" following the same explanation by WHITTEN in beetles. That would be quite improbable for this trachea will never serve the adult being completely shed at the final moulting.

MYERS (1928) uses frequently the term "praecostal area" for the usually narrow cell behind Pc in cicadas, finding it prominent in *Pycna* and *Yanga*. EVANS (1948) uses the same term refering to the wing pad of *Tettigarcta*. Despite this is the true pc cell, as both these authors do not recognize Pc, the term must have been introduced only as a borrowing from morphology of Fulgoroidea with "praecostal area" which superficially resembles the structure in Cicadoidea, thus using the therm by both authors is unrelevant to the correct identification of the cell. The next vein in the fore wing of Cicadoidea, CA+CP, was identified as Costa before the nodal line and as Subcosta behind the nodal line by MYERS (1928) and that was repeated by other authors. In HORVATH's opinion (in: MYERS, 1928) this vein is a continuation of Costa also behind the nl. Somehow both authors are right because the vein behind the nl is CP+ScP (Figs. 94, 97) as have been mentioned in the description above and will be explained further.

Axial unit — radial complex

This group of veins includes Subcosta, Radius, base of Media and Media Anterior (fused almost without trace to R). Through the axial unit the flying muscles in both wings transmit power, their action influences also the shape of a large part of the working surface of the fore wing during flight. In Cercopoidea a ridge on ScP helps to lock the fore wing on the pleuron at rest. Radius, flanked anteriorly, antero-basally or basally by ScP (usually recognizable only at the very base as a separate vein) and posteriorly by M is the central part of the complex. In the hind wing Sc is smaller but in a few examples of Fulgoroidea and Cicadelloidea its anterior branch was detected. When Sc is single it is only ScP as in all fore wings and also in hind wings of Cicadoidea and Cercopoidea. ScP looses its separate identity soon after the base but usually re-emerges distally, in most cases together with RA, joining or approximating CP. Radius is branched distally except in the fore wing of *Tettigarcta* and some Fulgoroidea where it branches near the base and in the hind wing of Cercopoidea and Cicadoidea. Certain taxons of lower rank show terminal reductions of ScP and branches of R. Media Anterior is found to exist as a remnant in some fore wings of Fulgoroidea, in all Cicadoidea and in the hind wing of many Cicadelloidea. Media Posterior leaves the radial complex soon after its base and here is treated as a separate unit. Basivenalia are fused to the veins of the axial unit except for MB in fore wing where it is separated from the vein (always fused to R basally) by a furrow.

Fore wing

Fulgoroidea. Subcosta Posterior (ScP)

The ridge extending antero-ventrally from the common stalk of the radial complex at base is ScP. The vein is visible only on the ventral side (Figs. 7, 175) but the wing membrane on the dorsal side is slightly depressed in the corresponding region that makes an impression of the existence of a (–) vein there. The depression of the membrane is deepened at the very base by the accompanying postcostal longitudinal line of flexion. The examples (Figs. 24, 74, 75, 86) show ScP as it can be observed in microscopic slides. The vein often bears a row of short setae on its basal part. In most of the wings ScP re-emerges from ScP+RA at about a level of tip of clavus and approximates CP (Figs. 43, 45, 69, 79) showing mildly negative (–) fluting. In Kinnaridae (Figs. 66, 68), Meenoplidae (Fig. 69) and especially in Cixiidae (Fig. 74) there is a strongly sclerotized, transverse vein, sometimes with a ventral ridge following the converging parts of CP and ScP. The region immediately behind the "cross-vein" is less sclerotized and it marks the costal end of the nodal line. The following composite longitudinal vein CP+ScP passes further into the
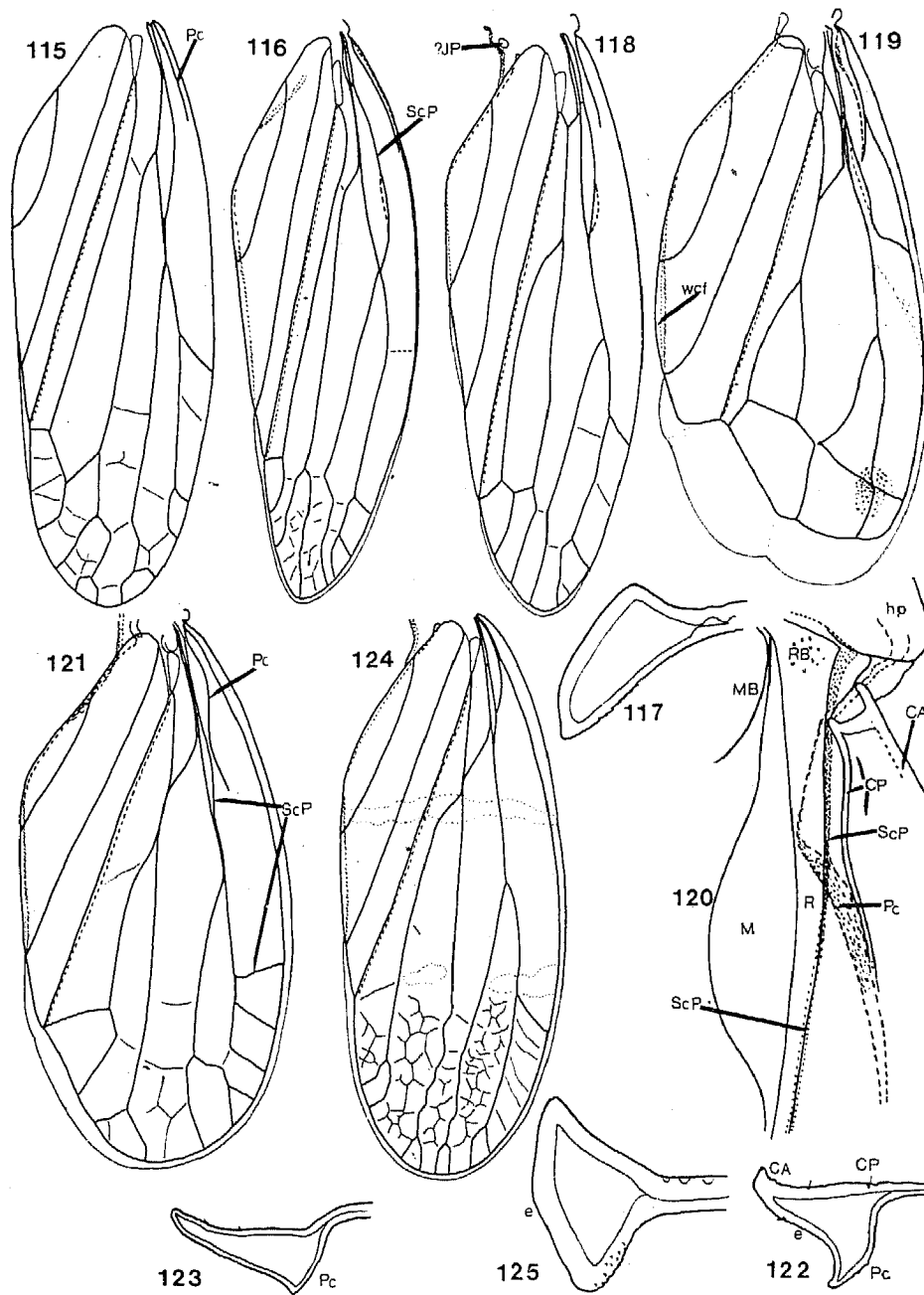
Figs. 115—125.
Ptyelus flavescens (F.): 115 — Aphrophoridae g. sp. (S. Africa): 116, 117. 117: subbasal cross-section through the costal margin — *Aphrophora*: 118 — *Clastoptera obtusa* (SAY): 119, 120. 120: basal attachment of veins in the fore wing up to M (other specimen) — *Locris*: 121—123. 122: basal cross section through the costal margin (compare with the Fig. 4) — 123: subbasal cross-section through the costal margin — *Prosapia bicincta* (SAY): 124 — *Philaenus spumarius* (L.), the cross-section through the site corresponding to that in Fig. 117): 125.

ambient vein (av) and all the subsequent longitudinal veins terminate on it. Sometimes a small fragment of the marginal membrane is detectable there (Figs. 39, 41). In most Delphacidae re-emerging ScP joins the composite costal vein but does not show any change in fluting (Figs. 81, 84). However in *Ugyops ?taraculae* (Fig. 79) it does and the conditions resemble these in Cixiidae and Achilidae. Among Derbidae there are numerous examples of intermediate conditions of the subterminal joining of ScP with CP (Figs. 50, 56—58, 64, 65). The region behind the junction of ScP and CP and the nl becomes slightly depressed, often contains a haemolymph lacuna and when it is pigmented, as in many Cixiidae and Delphacidae, it is called pterostigma. In the wings with Pc+CP vein, ScP (being richly branched) joins CA+CP to form the av (Figs. 24, 29, 30). In other wings ScP is a single vein terminally. In some non flying wings (Fig. 21) re-emerging ScP is neutral ($\pm$) or positive (+), in others it is obscure owing to reductions (Figs. 20, 23), reticulate venation (Figs. 9, 12, 32) or crowding of veins at the costal margin (Fig. 18). Certain difficulty with identifying of the re-emerging ScP is found in Dictyopharidae (Fig. 38) and Fulgoridae (Figs. 37a, 37b) where numerous veinlets show mildly negative fluting and all join the costal composite vein. Among the examined representatives of these families there was no distinct transverse line of flexion nor costal nodus but in some of them a pterostigma was present. Wings of some Derbidae (Fig. 52) slightly resemble the conditions of Dictyopharidae but in the former the single (—) ScP is easily detectable and the other veinlets ($\pm$) belong to RA. In *Redarator bimaculatus* there is a little vein emerging costally before the branching of R (Fig. 16). If this vein is identical with ScP this would be the only found example of nearly basal separation of this vein in Fulgoroidea. On the other hand in some fully winged Caliscelidae ScP has no separate identity from RA (Fig. 90) or disappears altogether (Fig. 87).

Radius Anterior (RA)

Radius basivenale is firmly fused to the vein, large, lamellate and provided with numerous sensillae. The prominent (+) common stem of the radial complex becomes levelled distally but for a long distance retains its placement parallel to the costal margin. After MP diverges and the rest of the veins bifurcate, ScP+RA continues its course parallel to the margin (Figs. 50, 58, 65, 74, 79) retaining at least mild convexity. When ScP leaves, the remaining vein ($\pm$) identified as RA remains single (Fig. 47), bi-branched (Fig. 56) or even multibranched (Fig. 43). In wings with Pc+CP vein, RA is multibranched (Figs. 24, 30). In many cases the numerous veins sprouting off RA costad are cross-veins (Figs. 64, 65) recognized as such owing to their lability. Often it is impossible to establish the true nature of the veinlets when the venation is reticulate (Figs. 9, 12) or even for certain discriminate them from ScP branches (Figs. 32, 38). Non flying wings of Delphacidae have RA as well as most of other veins as in flying wings (Fig. 83), in others RA is obscure (Fig. 21) or reduced (Figs. 18, 20, 23). In wings where ScP+RA branches subterminally RA turns mesad while ScP turns costad. This is a rule in Kinnaridae and Meenoplidae (Figs. 68, 69) where RA remains single, but occurs also in others (Figs. 33, 37e, 45). The reduced venation of some Caliscelidae shows RA as inseparable and undistinguishable from ScP (Fig. 90) or both are unrecognizable (Fig. 87).

Radius Posterior (RP) + Media Anterior (MA)

The next vein emerging from the radial complex anteriad after separation of MP is identified as RP being usually slightly lower than ScP+RA. This vein, however, has most probably a composite origin and includes also MA. In some wings there is distinct anterior stripe of thickened cuticle branching off anteriorly of MP at the point where it leaves the axial unit (Fig. 180). This remnant of MA is easy to trace along RP as a differently coloured stripe in *Scaralis. Hypaepa illuminata* also shows the presence of the anterior cuticular stripe contributing to the hind wall of the yet unbranched ScP+R vein. RP usually branches off before ScP separates from RA but there are exceptions (Figs. 16, 54). Branching of R
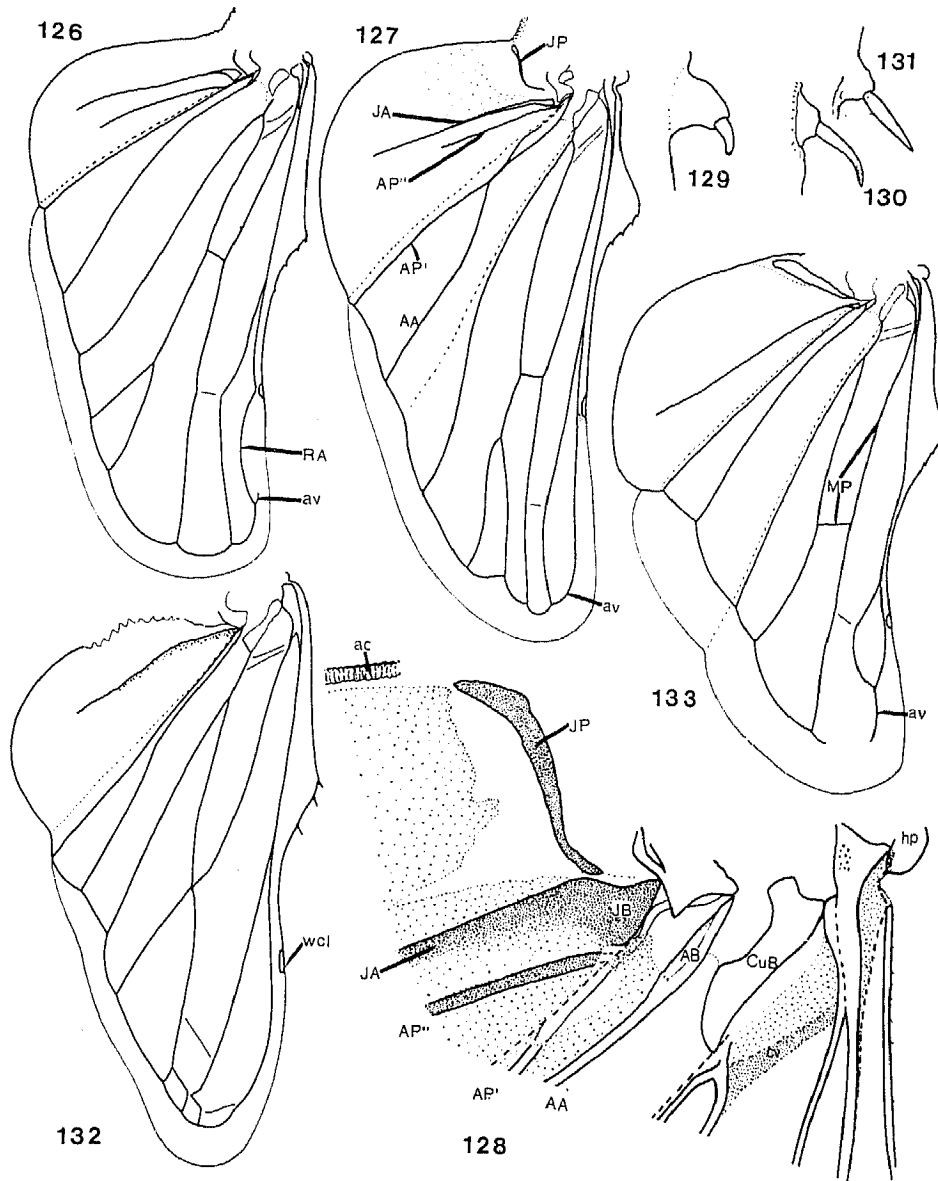
Figs. 126–133.
Locris: 126 — *Aphrophora*: 127, 128. 128: basal attachment of veins in the hind wing — *Prosapia bicincta* (SAY), sensilla at the expanded part of the costal margin of the hind wing: 129 — *Philaenarcys bilineata* (SAY): 130–132. 130 and 131: 2nd and 3rd sensilla on the costal margin in Fig. 132 — *Clastoptera obtusa* (SAY): 133.

takes place near base (Figs. 23, 39, 74, 79) especially in wings with Pc+CP (Figs. 24, 30) or more distally. RP usually turns mesad and in most of the examined wings it is bi-branched (Figs. 16, 39, 54, 57, 69, 79), but in large wings and these with Pc+CP vein it is multi-branched (Figs. 12, 24, 30, 43, 52, 74). In some non-flying wings (Fig. 23) and often when R branches subterminally (but not in Kinnaridae and Meenoplidae) (Figs. 37c, 90) RP is single. In most Delphacidae RP is also single (Figs. 80, 81, 84).

C i c a d o i d e a . Subcosta Posterior (ScP)

The vein is detectable and visible on ventral side as a comparatively low corrugation obliquely crossing the very base of the fused veins and R. It starts just in front of RB (Fig. 177) and looses its separate identity before the end of the "basal cell". The oblique furrow seen on the dorsal side, deep in singing cicadas (Fig. 178) and shallow and broad in *Tettigarcta*, traversing the base of the veins of the axial unit has no relation to the vein in question. ScP re-emerges as a rudimentary atracheate structure before the nl and joins C. Behind the nl the second branch of ScP joins the composite vein CP+ScP, more clearly visible in *Tettigarcta* (Fig. 97) and after joining RA it becomes av (Fig. 95). In singing cicadas the picture is more obscure owing to crowding of the veins (Fig. 94).

Radius Anterior (RA)

This vein is identified as the one gaining its separate identity behind the nl (while ScP re-emerges at the nl) and invariably having two terminal branches (Figs. 92, 93, 95, 102). In *Tettigarcta* the vein runs on a long distance before the nl as ScP+RA while in singing cicadas it is fused with RP+MA up to the nl.

Radius Posterior (RP) and Media Anterior (MA)

The common stem of the axial veins breaks off at the end of the "basal cell" where also the oblique furrow running subbasally across ScP+R and subsequently separating M terminates. In *Tettigarcta* there is a noticeable distance between ScP+R slightly arching anteriad and the straight M (Fig. 96) while in singing cicadas (Fig. 178) there is only a deep furrow. At this point MP turns mesad forming at least part of the "arculus" and MA fuses with ScP+R, being detectable before the fusion as a very short oblique or perpendicular branch (Figs. 96, 178). In *Tettigarcta* a vein distinctly negative in fluting branches off soon after (Fig. 95) while in singing cicadas the same vein branches off just before the nl (Fig. 94) showing positive fluting (Fig. 179). Detailed examination reveals that this is RP+MA, a single vein in all examples under study.

C e r c o p o i d e a . Subcosta Posterior (ScP)

The vein is basally fused to R (Fig. 120) like in Fulgoroidea, but it re-emerges on a short distance from the base being arched costad and bearing large sclerotized ventral extension (Fig. 116) which serves fastening the wing on pleuron at rest. The vein there is well visible on both sides of the wing (Figs. 115, 118, 121) being distinctly (–). Ventrally it comes into contact with the corrugation of Pc (Figs. 119, 121, 124) or not (Figs. 115, 118) but usually it turns back toward R. Only in *Clastoptera* (Fig. 119) ScP turns costad immediately after completing the usual arch. In the wings other than *Clastoptera*, venation is reticulate terminally that makes impossible identification of re-emerging ScP with certainty, although following a branch of trachea can be helpful.

Radius Anterior (RA) and Radius Posterior (RP) + Media Anterior (MA)

The vein situated mesad of arching ScP is R+M. After MP leaves the stem of R it includes, by comparison with Cicadoidea, also MA (however without a slightest sign of its physical presence) (Fig. 116). Then ScP re-joins (except in *Clastoptera*) the vein which immediately (Fig. 116) or after some distance (Figs. 118, 124) bifurcates into costal ScP+RA and mesal RP+MA. Morphologically none of these veins show its composite origin, they are midly (+) or (±). The anterior vein sends off costad (except in *Clastoptera*) various number of branches and usually forks terminally, the posterior one remains single or also

Figs. 134—147. ▶

Tartessini g. sp.: 134 — *Platycotis*; 135 — Membracidae g. sp.: 136 (from Venezuela), 137 (from Australia) — *Acutalis tartarea* (SAY): 138 — "*Ceresa borealis*", tracheation of the larval fore wing (after FUNKHOUSER, 1913); 139 — Cicadellini g. sp. (from Equador, total wing in Fig. 153): 140. Transverse cross-sections through the costal margin — *Bothrogonia*
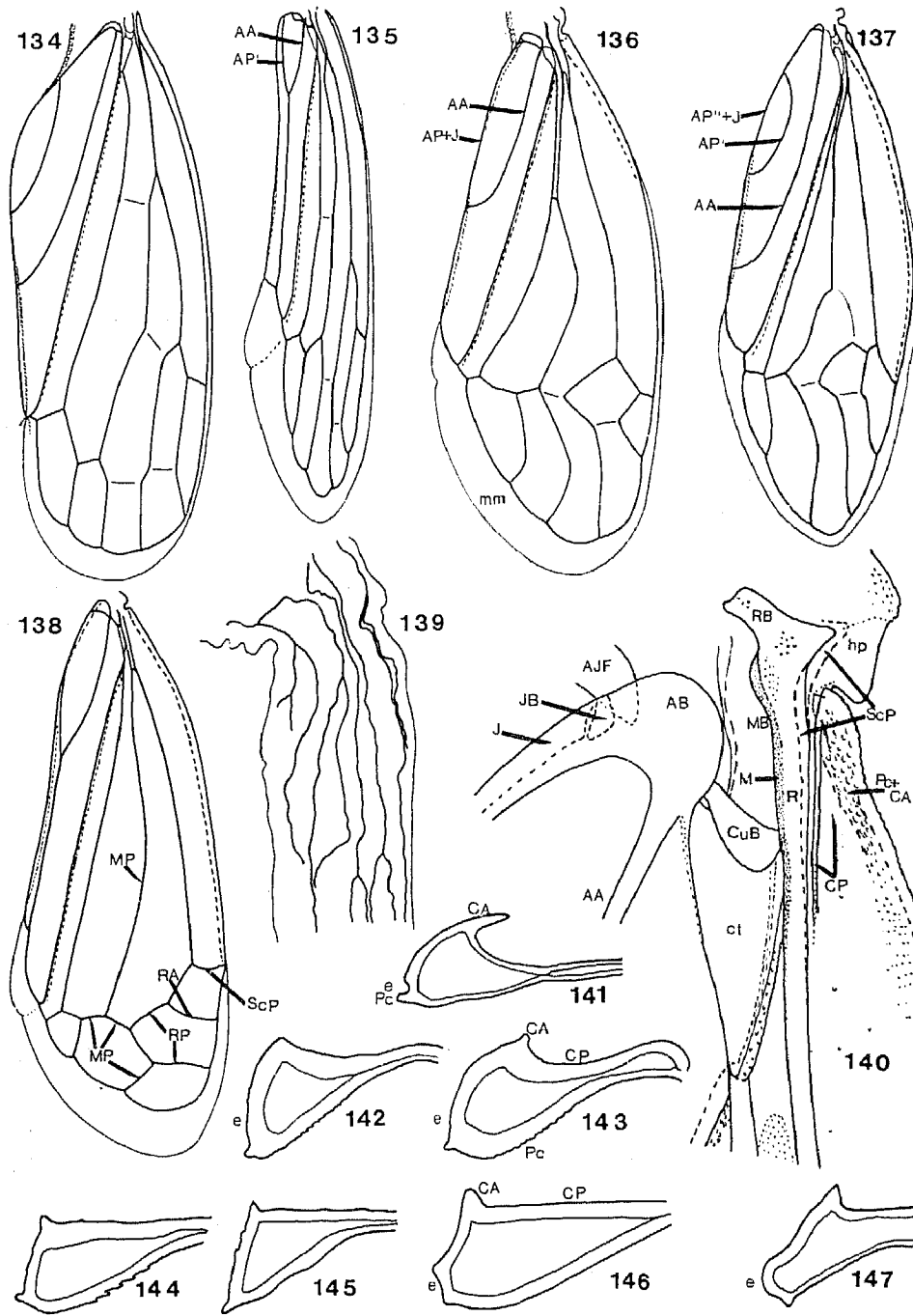
terruginea (F.), apicad of the cubital triangle: 141 — *Jikradia*, subbasal, basad of the end of the cubital triangle: 142 — *Oncometopia*, subbasal: 143 — Mileewaini g. sp. (Texas), subbasal: 144 — same, apicad of the cubital triangle: 145 — Xestocephalinae g. sp. (from Texas), ⅓ from base: 146 — *Kyboasca bipunctata* (OSH.), ⅓ from base: 147.

forks terminally if the venation becomes prominently reticulate (Figs. 115, 124). The first of the veinlets turning costad off the anterior branch can be identified, by comparison with Fulgoroidea, as re-emerging ScP (Fig. 124), the remaining ones, joining the composite costal vein, as veinlets of RA (resembling the arrangement in some Derbidae). Ambient vein is formed by fusion of the first veinlet of RA with the composite costal vein and it becomes accompanied by the marginal membrane which is often very narrow.

C i c a d e l l o i d e a . Subcosta Posterior (ScP)

The vein is strongly attached to RM stem anteroventrally in its basal part and retains its separate identity hardly behind the level of the end of the cubital triangle. In slides it is visible immediately mesad of the postcostal flexion line and the longitudinal sclerotization bordering CP (Fig. 140), Sc Basivenale turns toward the "humeral plate". In most wings there is a short vein branching off from RA subterminally and joining the costal vein (Figs. 135, 148, 154). By comparison with Fulgoroidea and Cercopoidea this short vein can be regarded as re-emerging ScP (sometimes it is mildly negative). In Typhlocybinae, some Idio-cerinae (Fig. 149), many Nirvaninae (Fig. 150) and some others there is only one vein compri-sing anterior branch of R and this vein can be identified as ScP+RA. In certain wings re--emerging ScP branches off before bifurcation of R (Figs. 138, 151).

Radius Anterior (RA) and Radius Posterior (RP)

After MP diverges from the common stem of the radial complex the composite vein con-tains ScP, R and MA (the last recognized under the same conditions as in Cercopoidea). Bifurcation of this vein takes place at about midlength of the wing (Figs. 135, 154), sub-terminally (Fig. 136) or terminally (Fig. 138). The anterior branch, including ScP, is a single vein but sometimes it sends off veinlets toward CP+ScP terminally (Fig. 148). The posterior branch RP+MA (the last one deemed to exist here only by comparison with Cicadoidea) is always single (Figs. 134, 136, 137). The mutual relations of RA and RP+MA remain the same whether ScP leaves before branching (Fig. 138) or after, or even when the separate ScP is not detectable (Figs. 149, 150).

Hind wing

F u l g o r o i d e a. Subcosta Anterior (ScA) and Subcosta Posterior (ScP)

Sc is situated latero-ventrally at the very base of R, extending considerably ventrad. At the very base of the vein there is usually a single row of rigid macrosetae (Fig. 42), directed ventro-mesad. The setae are few in number and big or slender but numerous and only seldom they are situated on base of R, in Ugyops ?taraculae the setae were on base of M and in one unidentified Cixiidae species from Galapagos they were absent. In some of the wings behind the part of Sc bearing the macrosetae there is a short anterior vein fusing with Costa while the posterior vein still remains detectable. Thus the anterior branch is considered to be ScA and the posterior one (the only part of Sc easily detectable in majority of wings) as ScP. The trace of ScA is found in Ricania fenestrata, Acanalonia, Hemithiscia, Epiptera pallida, Enchophora, some species of Cedusa and ?Elidiptera (Fig. 42) and it was vaguely present in Colpoptera and Dictyophara from S. Africa. On its fur-ther course ScP is fused with R and eventually re-emerges at wcl. The only distinctly separate re-emerging ScP is found in Enchophora (Figs. 37c, 37d) where it is mildly (—). In other wings there is one (Fig. 25) or more (Figs. 31, 34, 44) veinlets being (±) or (—) branching off from RA and joining Costa. They (or at least one of them) might represent ScP with a degree of probability similar to that in the fore wing of Dictyophara. In most other wings there is only one vein branching off from ScP+R+MA costad — and this vein, usually (—), must contain ScP (Figs. 15, 59—62). In wings with reduced venation ScP may not re-emerge (Fig. 88) as is often in non flying wings (Fig. 22). In all wings, with the exception of Tettigometridae, the anterior branch coming from the radial stem, identi-fiable as ScP+RA, joins Costa and gaves rise to the av (Fig. 67).
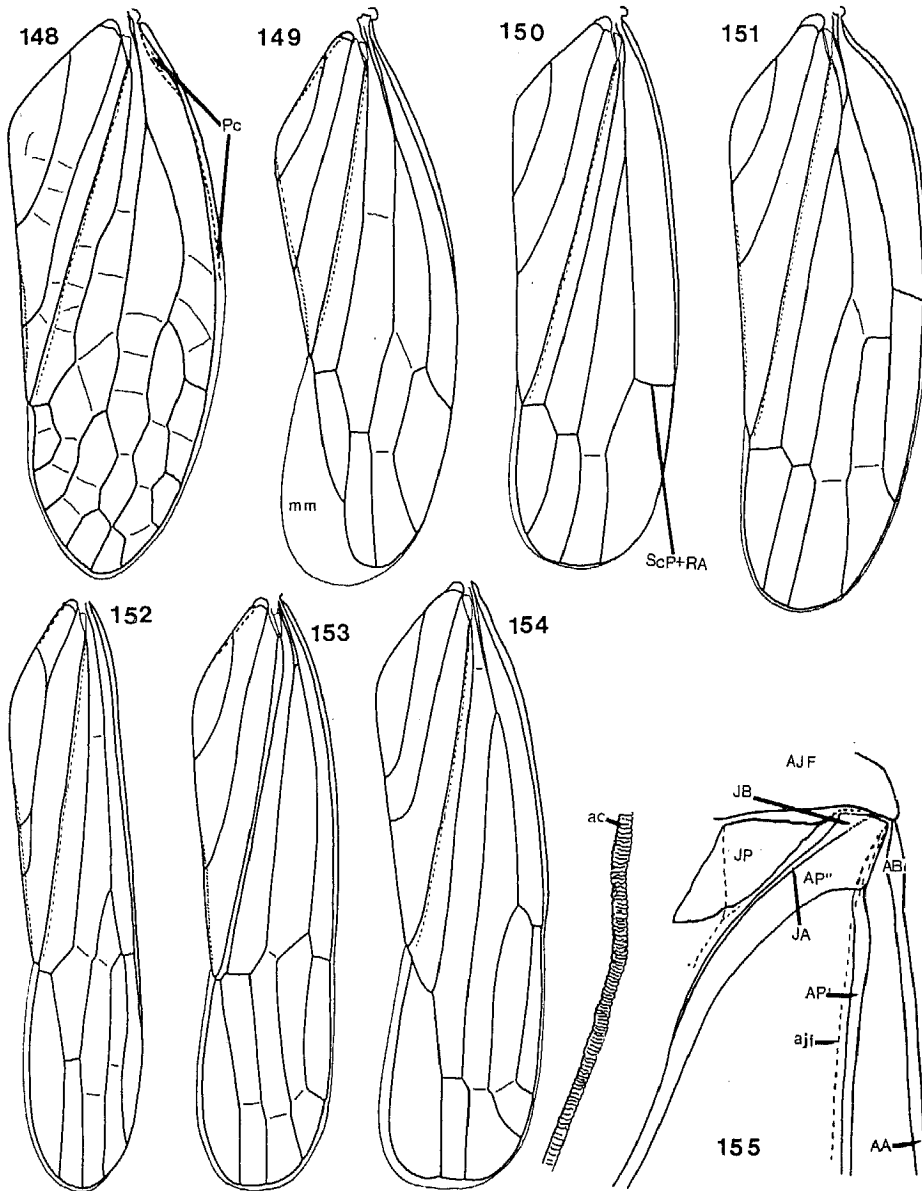
Figs. 148—155.
Coloborrhis corticina (GERM.): 148 — Idiocerinae g. sp. (Australia): 149 — Nirvaninae (from Equador): 150 — *Agalliopsis*: 151 — *Dichrophleps*: 152 — Cicadellini g. sp. (from Equador): 153 — *Ciminius hartii* (BALL): 154 — cicada from Venezuela, basal attachment of the veins of ano-jugal complex in the hind wing: 155.

Radius Anterior (RA) and Radius Posterior (RP) + Media Anterior (MA)

The radial stem bifurcates at wcl and the anterior branch is ($\pm$) after it sends off (—) veinlets toward Costa (Figs. 31, 34, 44) or mildly negative if it remains as a single vein (Figs. 15, 59—62). The former case represents ScP+RA and, terminally RA, the later

one a single ScP+RA. *Enchophora* (Fig. 37c) and maybe most Fulgoridae have RA separate from ScP and at least sometimes branched. In non-flying wings RA is detectable by its position whether a trace of ScP is present or not (Fig. 22) but in some flying wings with reduced venation it is undistinguishable (Fig. 88). In all wings, except Tettigometridae, there is av resulting from fusion of ScP+RA or RA with Costa (or rather CP) (Fig. 67). The posterior vein bifurcating off from the radial stem is idebtifiable as RP+MA despite there is no morphological trace of MA except of its influence on fluting which is (+) basally and ($\pm$) terminally. RP in most of wings is a single vein (Figs. 15, 34, 36, 61) easily detectable even in non flying wings (Fig. 22) but in wings with broadened apex it can be bifurcated (Fig. 37) or even multibranched (Figs. 25, 31, 37d, 44). Flying wings with reduced venation can have a single vein identifiable as ScP+ R+MA (Figs. 88, 89).

Cicadoidea. Subcosta Posterior (ScP)

The vein is visible at its start as a ventral swelling at the common base of the axial veins (Fig. 111) and has separate identity only on a short distance from the base, recognizable only on the ventral side of the wing. In slides of wings of singing cicadas there is an extension at the base of the vein joining Costa, it might represent ScA (Fig. 107). In singing cicadas ScP usually re-emerges as the ascending part of the veinal arch situated at the wcl (Fig. 114). On the top of the arch the vein takes a haemolymph volume from the costal complex through a lacuna (Fig. 104). The descending part of the arch is identified as CP+ScP (Fig. 114) for a trace of CA is found at the very margin behind the wcl in some large wings (Fig. 113). The remnant of CA fades off into the marginal membrane and the first vein at the costal margin containing initially CP, ScP and RA is the av. In *Tettigarcta* (Fig. 112) the ascending part of the arch is hard to detect, instead ScP is immediately fused to the veins of the costal complex. However, the descending part of the arch, identifiable as CP+ScP (Fig. 108), is quite long (Fig. 106).

Radius Anterior (RA)

The vein is fused with ScP and re-gains its separate identity only between point of the divergence of ScP and join the composite vein CP+ScP. Thus RA as a separate vein can be seen between ends of the arch at the wcl and it is minute in singing cicadas (Fig. 101) and long in *Tettigarcta* (Fig. 108). Behind the arch the av starts.

Radius Posterior (RP) + Media Anterior (MA)

In *Tettigarcta* a hind branch leaving Sc+R very near the base is depressed on dorsal side, in the ventral view (Fig. 111) it shows connection with MB and with diverging MP. In singing cicadas (slides) there is a sclerotized elevation on the dorsal side arising from the MB and joining R at its base. This elongated sclerotization, situated over MP is the anterior branch of M and it becomes incorporated into the RP. In *Okanagana* (Fig. 107) the arrangement in this region is very similar to that of *Tettigarcta*, the picture is only more obscure owing to desclerotization of RP and MP at base. In most of the singing cicadas the coalescence of RP+MA with MP occurs on a long distance looking like a stem of one vein (Fig. 101). The vein RP+MA usually branches terminally (Figs. 106, 108) serving the very tip of the wing, sometimes remains single (Fig. 105). On the theoretical grounds the hind branch in the wings with bifurcated RP+MA can be identified as MA.

Cercopoidea. Subcosta Posterior (ScP)

The vein consists of a broad base and a minute corrugation on a very short distance antero-ventrally at the base of R+M. Subsequently it exists only vaguely recognized because of comparison with Cicadoidea and presence of traces of the costal part of the av (Fig. 126) and a subcostal branch of trachea in some Cercopidae. In *Ptyelus* there is a perpendicular vein behind the wcl, most probably a cross-vein.
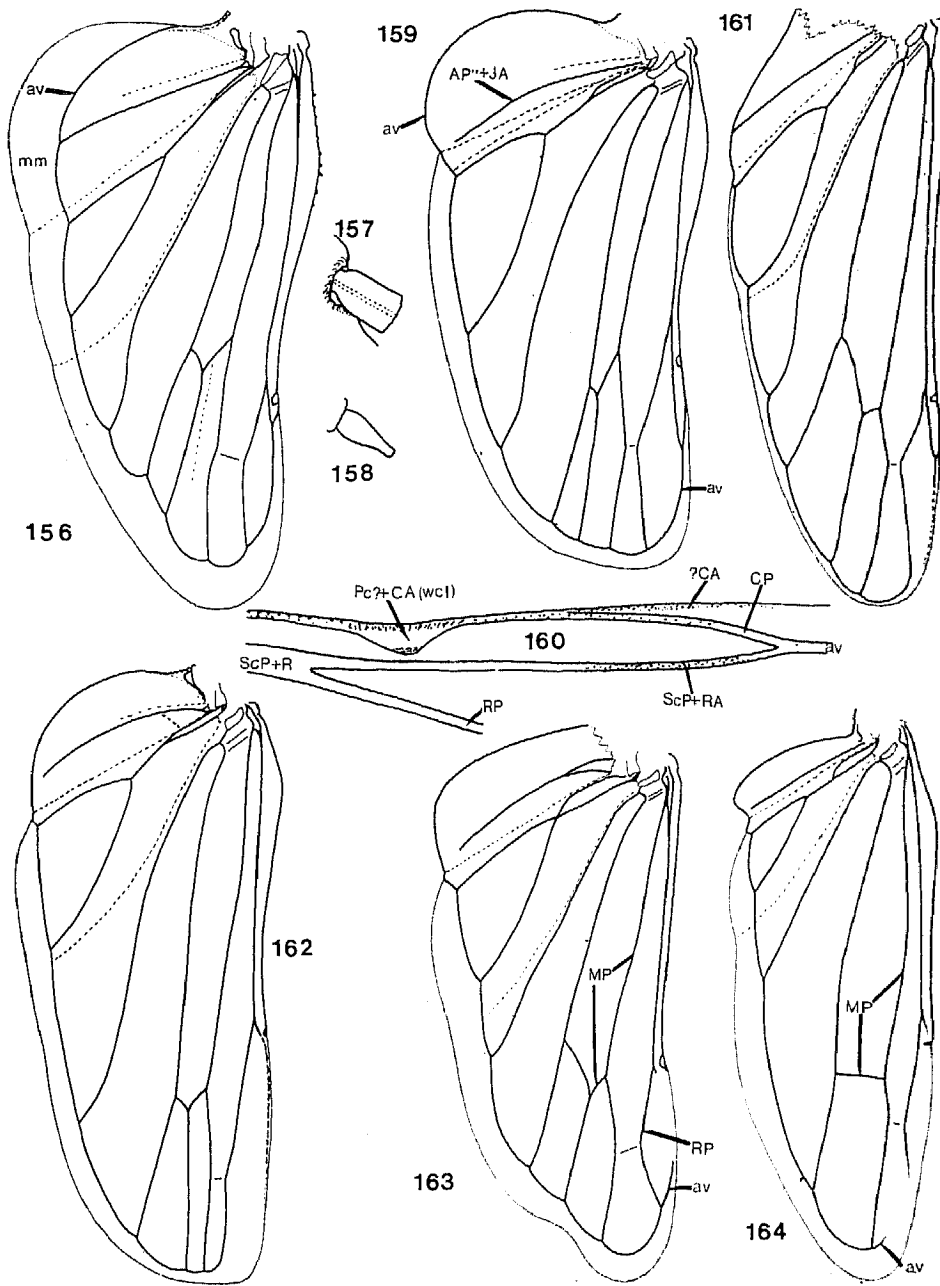
Figs. 156—164.
Tartessini g. sp.: 156—158. 157: sensilla at the costal margin of the hind wing seen at its broader surface — 158: same, seen from the edge — *Ponana*: 159, 160. 160: region of the wcl, the costal margin turned up (compare with Fig. 67) — *Dichrophleps*: 161 — *Ciminius hartii* (BALL): 162 — *Coloborrhis corticina* (GERM.): 163 — *Joruma*: 164.

Radius Anterior (RA) and Radius Posterior (RP)

The stem ScP+R bifurcates quite near the base, always basad of the wcl (Figs. 126, 127, 133). The anterior branch (RA) is (+) or (±), the posterior one (RP) (—), both unbranched. The av starts when both these veins merge together except in some Cercopidae where costad of RA a remnant of the av takes the volume of the haemolymph from an obscure lacuna at and behind the wcl (Fig. 126). Because the coalescence of R and M at base is compact it is impossible to detect any trace of MA.

C i c a d e l l o i d e a . Subcosta Posterior (ScP) + Radius Anterior (RA)

Basally ScP is inconspicuous and the best visible in slides (Fig. 168). In all examined insects the stem ScP+R+MA bifurcates in the vicinity of the wcl and the anterior branch, identified as ScP+RA, turns slightly costad and meets a vein which by comparison with Fulgoroidea is CP but (±) or (+). After fusion of these veins the av starts (Figs. 159, 160). Sometimes the forming of the av is modified (Figs. 161, 162) and in some wings ScP+RA is strongly reduced (Fig. 163). Development of this vein in *Coloborrhis* resembles the picture in Cercopoidea but the veins involved are not homologous. In many Typhlocybinae ScP+ RA is obscure or seems to be totally reduced (Figs. 164—166).

### Radius Posterior (RP) + Media Anterior (MA)

The base of R vein is fused with MB (Fig. 168) and in many wings (well visible in slides of wings of Typhlocybinae) there is a strongly sclerotized rod originating on MB and merging with R. This structure being fused with basivenale and situated above the diverging MP (—) is identified as MA. Thus the hind branch after bifurcation of the veins of the axial unit is found to be RP+MA. While branching off at the wcl the vein is (±) or (+) and always single. It joins av separately (Figs. 156, 159) or being fused terminally with MP (Figs. 165, 166).

Discussion of the axial unit — radial complex

It results from the above study that ScA have merged with veins of the pronating unit (Fig. 42). As a vein it is detectable only in hind wing because of the necessary desclerotization of the postcostal flexion line in fore wing.

The idea of fusion Sc with C or rather replacement C by Sc was developed by those who have identified veins as tracheae (FUNKHOUSER, 1913; METCALF, 1913a; MUIR, 1923 in: FENNAH, 1944; DAVIS, 1961, in part) and was followed by many others. This led to incorrect identification of the composite costal vein in Cicadelloidea as Sc that was discussed above. HESLOP-HARRISON (1955b) accepts presence of ScA and ScP suggesting that the anterior branch joins Costa. His description is so clear as if he would be looking at the wing shown here in Fig. 42. However, the brilliant writing miss the point if to realize that it is dealing with the fore wing and, moreover, out of the 9 illustrations in his paper only that of Psyllina follows the idea. SNODGRASS (1935) recognizes "humeral cross vein" as the constant element between Sc and C and gives the examples of Plecoptera and Mecoptera where this vein is actually descending part of ScA. EMELJANOV (1977) mentions the vein in question calling it "hamulus" while summarising his view on veins of insects in general but does not give any example among Auchenorrhyncha.

Mesosoic Palaeontinoidea (SHCHERBAKOV, 1984) show very clearly presence of MA which fuses with RP (BECKER-MIGDISOVA, 1962). In the fore wing of *Suljuctocossus prosboloides* BECK.-MIG. (op. cit. Fig. 437) there is a basal fusion and then RP+MA runs as a single vein parallel to RA. In the hind wing of *Shurabocossus gigas* BECK.-MIG. (op. cit. Fig. 443) the veins in question fuse with each other subbasally into RP+MA and then diverge. Both these examples are of Palaeontinidae while Dustaniidae (SHCHERBAKOV, 1984) show the picture which is transitional toward Cicadoidea. Thus is follows that it is highly probable that the hind branch of "RP" in the hind wing of Cicadoidea is re-emerging
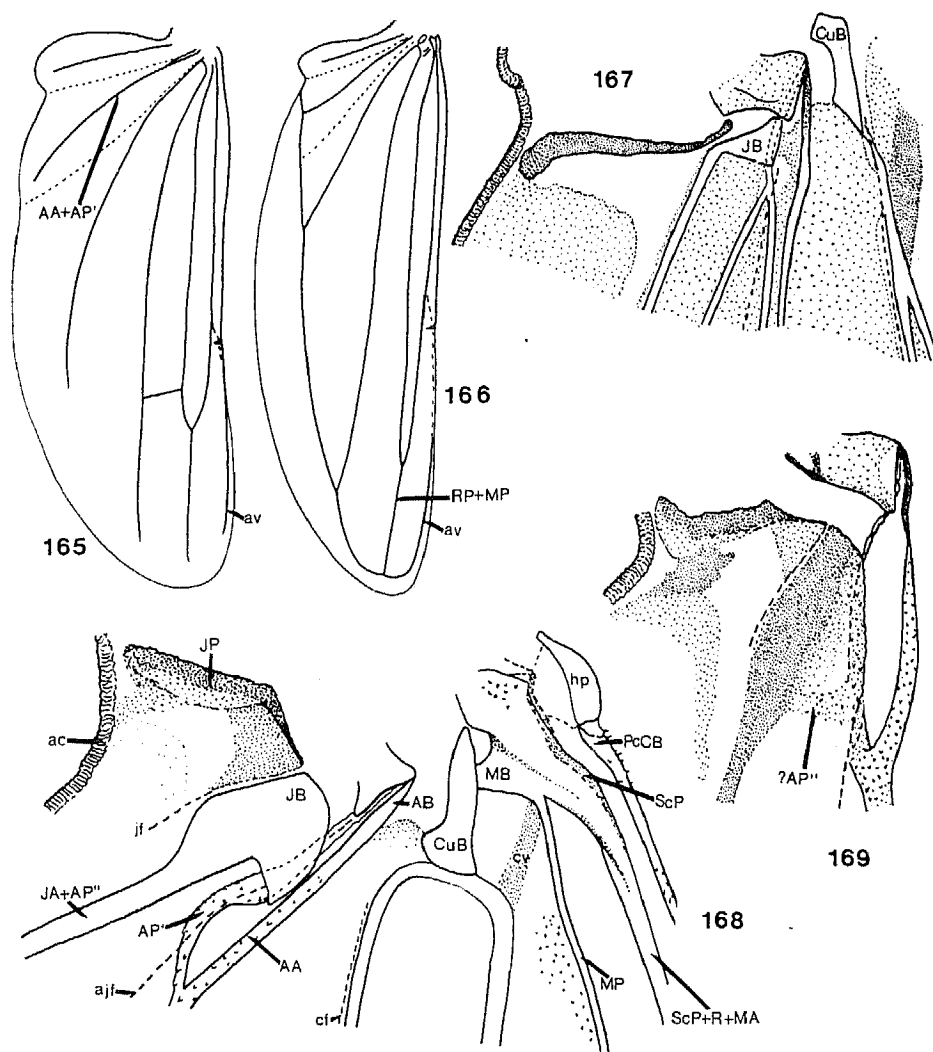
Figs. 165—169.
Diomma pulchra (MATS.): 165 — *Kamaza reducta* DWOR.: 166 — *Philaenus spumarius* (L.), basal attachment of veins of ano-jugal complex (more explanations in Fig. 128): 167 — *Balclutha*, base of the hind wing: 168 — *Ciminius hartii* (BALL): 169.

MA. Fusing RP with MA is not an unique character of Cicadoidea, their ancestors nor even Auchenorrhyncha. The fusion is clearly visible in the hind wing of beetles (Fig. 29, terminal R_2-R_4 in: EMELJANOV, 1977), in Sialidae (original observation) and, slightly obscured, in Corydalidae of Megaloptera (KUKALOVA-PECK, 1983, Figs. 17A and 17B).

Several authors noticed a separate vein turning costad off the radial stem, e. g. "nodal vein" in *Oncometopia* (COMSTOCK, 1918), "nodal cross-vein" in Cicadelloidea (METCALF, 1913a) but it was seldom interpreted as re-emerging Sc (e. g. in the fore wing of *Cixius* in: DAVIS, 1961). Most of the troubles with interpretation resulted from the acceptance, after COMSTOCK and NEEDHAM the scheme of 5-branched Radius based on tracheation of larval wing pad of *Magicicada septendecim*. So, the R_1 (identified with the larval trachea that is lost in adult) is commonly present in literature and at the same time no one

bothers about simultaneous "loss" in adult of one branch of the subcostal trachea (also present in the same larval wing pad). Analysis of the arranngement of adult veins at the costal nodus of singing cicadas indicates that the anterior branch of subcostal trachea has been lost in adult and the second branch (weaker in the wing pad) is the only trachea serving posterior branch of re-emerging ScP while its anterior praenodal branch remains atracheate (Fig. 94, see also COMSTOCK, 1918). FENNAH (1944) calls "nodus" a point where re-emerging Sc joins end of C and states that stigma is an area enclosed by the margin of wing and distal veinlets of Sc (he erred interpreting also two branches of RA as Sc in *Mnemosyne*). HESLOP-HARRISON (1955b) finds it hard to accept because it would involve too many changes in interpretation of other veins (he means labeling Sc as above).

Interpretation of branching of R was affected by acceptance the COMSTOCK-NEEDHAM scheme (FUNKHOUSER, 1913; METCALF, 1913a, 1913b, 1917; MYERS, 1928; ZALESSKY, 1944; DAVIS, 1961, in part) which led to great diversity of patterns followed at random by other authors. The only exception is HESLOP-HARRISON (1955b) who promptly denies existence of 5-branched R. HAMILTON (1972a) finds the radial vein primarily containing two separate veinal units — Radius and Sector basing on venation of Odonata after FOR-BES and paper by ZALESSKY. Then, perhaps after acceptance of the loss of the first branch of radial trachea as the COMSTOCK-NEEDHAM scheme implies, and comparison with the tracheation in Cercopoidea (after METCALF, 1917) he concludes "Radius is atrophied leaving only Sector". The former interpretation of veins in Odonata proved to be incorrect (KUKALOVA-PECK, 1983, Figs. 16B, 16E) and the examples given by ZALESSKY (1944) who claimed confirmation of the dual character of Radius do not match this belief. The remark by KUKALOVA-PECK (1983) that in Neoptera RiA and RP are fused perhaps does not intend to emphasize distinction between the two groups for the two branches of R are fused also in some extinct Palaeoptera, even on a longer distance than in hind wing of Cicadoidea.

EMELJANOV (1977) states that R has two branches and the third Sc+R_1 and finds similarity of the arrangement in Recent Auchenorrhyncha with Permian Prosbolidae. Similarly, the 3-branched R is accepted by WOOTTON & BETTS (1986) when they propose another archetypal venation of Auchenorrhyncha based on the fore wing of *Permocicadopsis angustata* MART. and on the hind wing of *Prosbole ioagorae* BECK.-MIG., both Permian Prosbolidae.

The two above interpretations are near to the pattern found in the present study with the difference that the first of the three branches of R in their schemes is re-emerging ScP and that RP contains a component derived from M. In various lineages secondaries of almost each vein can develop, even in RA of the hind wing of cicada e. g. *Cystosoma saundersi* WESTW. (EVANS, 1956) and commonly in both wings of Fulgoroidea.

EMELJANOV (1977) is the first who recognizes presence of the av in both wings of all Auchenorrhyncha and discriminates the marginal membrane as separate from av. Originally he links its origin with one of the "keels" on the composite costal vein. My studies confirm this and the "keel" is identified as CA. If to accept that Pc turns dorsad and terminates on the wcl, the marginal membrane can appear only behind the wcl in the hind wing what is actually the case. In the fore wing where Pc turns ventrad, potentially the marginal membrane can appear at any point, even before the "costal nodus" as is the common place in Membracidae.

<div align="center">Transitional unit — Media posterior (MP)</div>

Distinguishing this unit is owed to its comparatively large area which is, unlike the axial unit, mostly passively deformed during flight. When wings are folded over back MP is pulling and pushing the neighbouring areas through its connections with R and Cu and this substantiates the name "transitional". MP is almost always (–) basally and in Fulgo-
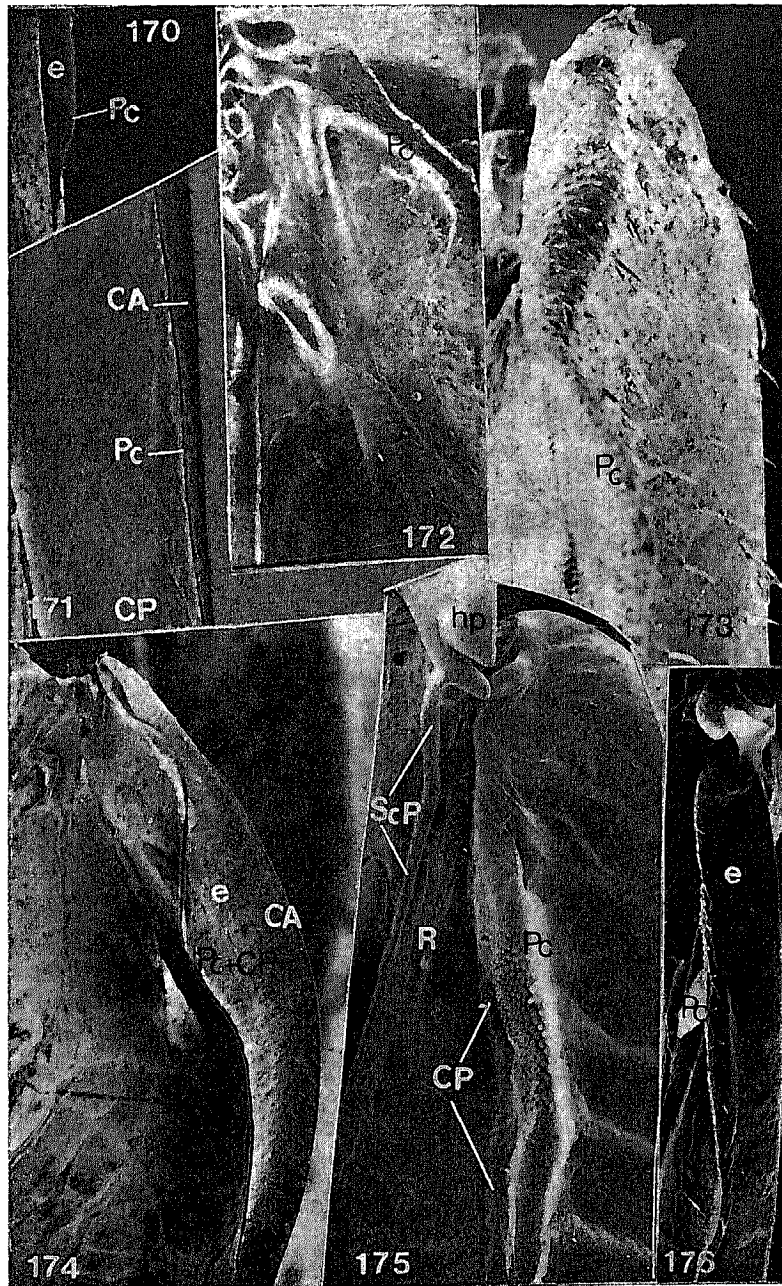
Figs. 170—176.
Sivaloka, dorsal side of the fore wing, Pc unfolded: 170 — *Colpoptera*, the region of the end of Pc (dotted in Fig. 11) shown from the edge in the ventral view: 171 — *Delhina*, ventral side of the base of the fore wing (total in Fig. 9): 172 — *Colmadona testudinaria* (DIST.), ventral side of the costal region of the fore wing at base (total in Fig. 12): 173, 174 — *Ormenis*, basal attachment of Pc+CP composite vein and veins of the axial unit, ventral side (compare with Figs. 7 and 86): 175 — *Pelitropis rotulata* Van D., ventral side (Pc seen from its edge displaying the reversed scale sculpture, demarcation line visible on epipleuron to the right): 176.

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roidea often richly subbranched. In the hind wing it is fused to MB, which is fused to RB. In the fore wing a desclerotized furrow separates the vein (fused to R) from its first sclerite of dorsal articulation. Subbasal coalescence with CuA is discussed later.

Fore wing

Fulgoroidea.

The most abundant branching is found in Fulgoridae (Fig. 37a). In this example MP sub-branches 7 times terminating on above 20 secondaries. The lowerst number of terminal branches in shown in Fig. 79 and the intermediate examples are easy to find among dra-wings, sometimes 4 terminal secondaries occur (Fig. 37e). The vein is usually free but sometimes it coalesces terminally (Figs. 51, 65) or subterminally (Fig. 18) with CuA.

Cicadoidea.

After leaving the radial complex the vein forms partly or completely the "arculus" (Figs. 93, 102). MP usually branches once before the nl and once behind the nl sending off 4 terminal secondaries. The almost reticulate venation of *Polyneura* is made exclusively by MP branching 3 times before and at least 3 times behind the nl.

Cercopoidea.

MP is bi-branched terminally where it usually coalesces with CuA. With few exceptions (Figs. 115, 116) it also coalesces subbasally with CuA and re-emerges later (Figs. 118, 119), the terminal branching is often obscure (Figs. 116, 121, 124).

Cicadelloidea.

Sometimes the vein coalesces with CuA subbasally and re-emerges more apically (Figs. 136, 151). It is bi-branched terminally and in most wings the hind branch coalesces with CuA (Figs. 134, 138, 149), rarely it is free (Fig. 148).

Hind wing

In all superfamilies MP is bi-branched, in Fulgoroidea sometimes multibranched (Figs. 37d, 44). In Fulgoroidea with highly intergrated venation (Figs. 15, 76, 82, 89) in all Cicadelloidea (Figs. 156, 163, 164) and in Cercopoidea (Fig. 127) the hind subbranch coalesces with the subbranch ofCuA terminally. In some Cicadelloidea the anterior branch coalesces terminally with RP (Figs. 165, 166).

Discussion of the transitional unit — Media Posterior

The idea of the veinal pairs of the alternative (+) and (—) fluting was developed by LAMEERE (1923) who, anticipating concavity of Media in Homoptera, recognized it as MP. The additional support he drove from the fact of large veinless surface in front of M in reduced "homopteran" venation of *Scytinoptera kokeni* HANDL. when compared with the "complete" venation of *Lycocercus goldenbergi* BRON. HESLOP-HARRISON (1955a) considers M as including MA and MP when bi-branched and as MA when single (in some Psyllina). Media is complete vein because, in his opinion, medial trachea is always bi-furcated and the vein often branches symmetrically. In the actual fact MP (except in Cicadoidea) seldom branches symmetrically, bifurcation is the only possible way of sub-branching and in Cercopoidea the medial trachea is single.

Determination Media as MP in the present study is based on presence of a remnant of MA fused to R and basal fluting of the system. The short vein between MP and CuA in the hind wing of Cercopoidea is recognized as part of MP following the 1st major criterium of homology while compared with Cicadelloidea. Similarly is interpreted the terminal coa-lescence of MP with CuA in the fore wing, with the additional support from innervation
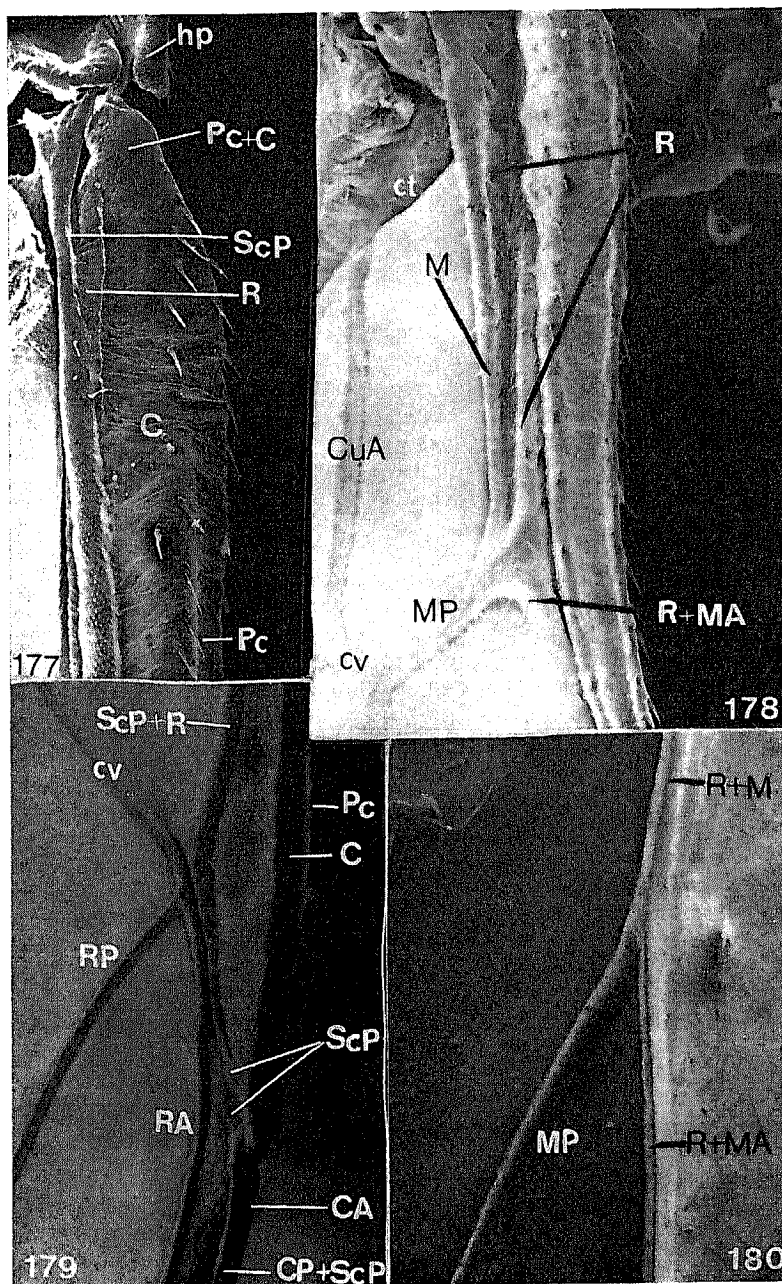
Figs. 177—180.
? *Taipinga*, basal attachment of veins of the costal and radial complexes, ventral side: 177 — ? *Taipinga*, surrounding of the "basal cell", dorsal side: 178 — ? *Taipinga*, costal nodus, dorsal side (compare with Fig. 94): 179 — *Nersia*, emerging of MP in the fore wing (MA continued along the hind wall of R), dorsal side: 180.

(ZAĆWILICHOWSKI, 1936). Thus MP is considered as bi-branched terminally in Cercopoidea. The basal coalescence of MP with CuA occurs within all superfamilies (Fig. 35) and sometimes is a labile character (e. g. *Lepyronia coleoptrata* (L.) — EMELJANOV, 1977).

WOODWARD et al. (1970) states than in Cercopoidea Media is "never proximally associated with R" and EVANS (1948) writes that in *Xiphistes tuberculata* (WALK.) of Membracidae M is not fused to R as a primary condition. The present study indicates that the Australian authors must have recognized beginning of the vein distad of its base.

Plical unit — Cubitus (Cu)

Cubitus is functionally connected with clavus. The name of the unit is referring to the very elaborate plication that takes place along the claval furrow during flight. Mildly (+) CuA, (—) (at least in the hind wing) CuP and in the fore wing a part of the membrane cut off by flexion lines at base, the cubital triangle (SHCHERBAKOV, 1984) belong to this unit. Basivenale in the fore wing is separated from the vein by a desclerotized space but in the hind wing it is connected. In the hind wing Cu is active while folding the wings over back, the area is rather passively deformed during flight.

Fore wing

In all superfamilies CuA is basically bi-branched terminally and CuP single and, at least subterminally, occupying the edge of clavus. Fulgoroidea show exceptions where CuA is single (Fig. 13) or multibranched (Figs. 24, 43). In Fulgoroidea CuA usually branches basad of tip of clavus and its secondaries serve hind apical angle area (Figs. 52, 68, 79), usually a cross-vein between CuA and CuP or CuA and av marks the tip of clavus. In three other superfamilies and in some Fulgoroidea (Fig. 51) the posterior branch of CuA runs toward the tip of clavus joining av. The anterior subbranch of CuA is free in Fulgoroidea (Fig. 16), Cicadoidea (Figs. 93, 95), some Cercopoidea (Fig. 116) and e. g. *Coloborrhis* of Cicadelloidea (Fig. 148) but it coalesces with MP terminally in all remaining Cicadelloidea, Cercopoidea and some Fulgoroidea (Figs. 51, 85). There are examples of subbasal coalescence of CuA with MP within all superfamilies (Figs. 18, 102, 118, 151). Examples of extraordinary arrangements at the tip of clavus in Fulgoroidea are given at description of the next unit. Non-flying wings with reduced venation retain typical branching of CuA (Figs. 18, 20, 21) while CuP is sometimes reduced.

Hind wing

The common stem behind CuB is usually short (Figs. 44, 159) but sometimes it is long (Figs. 59, 60) or reduced (Fig. 156). In some Fulgoroidea CuA is multibranched (Figs. 34, 44), in most Typhlocybinae of Cicadelloidea it is single (Figs. 164, 165). In Cicadelloidea (Figs. 156, 164), Cercopoidea (Figs. 127, 132) and Fulgoroidea with reduced (Figs. 88, 89) or highly integrated venation (Figs. 76, 82) the anterior branch of CuA coalesces with MP, in some Issidae the hind subbranch of CuA coalesces also with CuP (Figs. 14, 15, 17).

Discussion of the plical unit — Cubitus (Cu)

Recognition of the first vein on clavus as the same as hind subbranch of Cu in the hind wing we owe TANAKA (1926, in: DAVIS, 1961) although already MUIR (1923, in: FENNAH, 1944) correctly identified it in Fulgoroidea. In the present study the direct evidence of the morphological unity of both cubital veins in the hind wing is provided by haemolymph channels, marked by naturally pigmented haemolymphocytes flowing from CuB through the common stalk and then into both branches (Fig. 181). In the fore wing the varied degrees of the advancement in cutting off CuP from CuA by the claval furrow are demonstrated in singing cicadas (Figs. 98—100) and Ciciidae (Fig. 75). The "final" situation of CuP on the edge of clavus is found in *Tettigarcta* (Fig. 103) as well as in all other superfamilies. HAMILTON finds two veins on sides of the claval furrow (HAMILTON, 1972b,
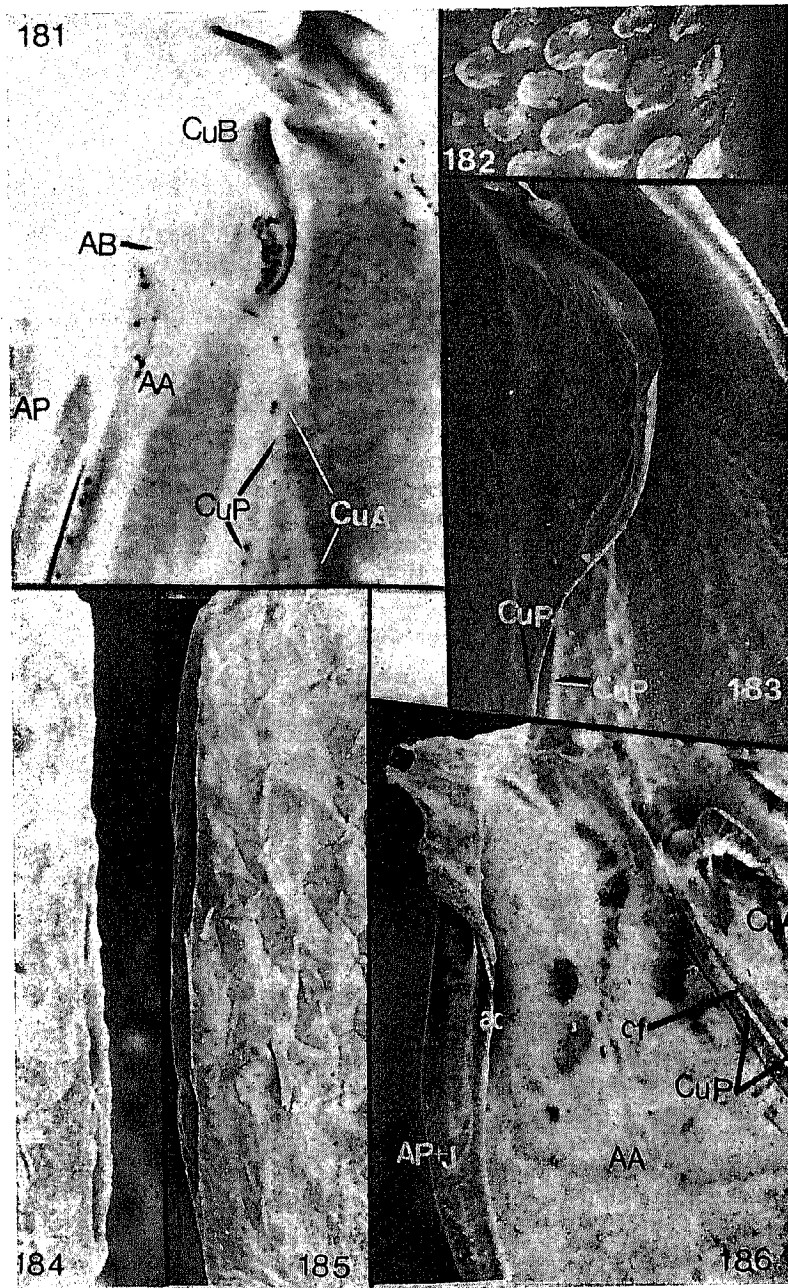
Figs. 181—186.
Cixiidae g. sp., microscopic slide of the hind wing in Euparol, roundish haemolymphocytes pigmented: 181 — *Eparmenoides*, reversed scale sculpture on the ventral side of unfolded Pc, edge to the right: 182 — *Balala*, ventral side of the fore wing at the base of CuP: 183 — Caliscelidae g. sp. (S. Africa), "tonguing and grooving coupling device" of the non flying wing made by Jugals, groove: 184 — tongue: 185 — *Colmadona testudinaria* (DIST.), base of clavus detached from basal articulation, ventral side of the fore wing (total in Fig. 12): 186.

Fig. 16). If to consider the examples cited above it is evident that he takes CuP, split longitudinally by the claval furrow (Figs. 183, 186), for two veins. The praeclaval parts of CuP are quite distinct in some wings through all superfamilies.

Vannal unit — anojugal complex

The name of the unit derives from "vannus", a fan-like expansion mentioned by SNOD-GRASS (1935) in the hind wing. The unit is comprising AA, AP, JA and JP in the hind wing and one jugal vein in the fore wing. In the hind wing the vannal unit is bordered by claval fold and its area is traversed by anojugal and up to 3 jugal folds. In the fore wing there are two obscure folds at the base of J and sometimes others, even more obscure, in these Cercopoidea which have a sclerotization on the "jugal membrane" (Fig. 118). The vannal unit is active during folding wings over back, in the hind wing it creates large working surface and in the fore wing it provides the wing coupling fold (wcf) (OSSIANNILSSON, 1950) made by a subterminal part of J while more basal part of J forms an extension which fits into the scutellar groove at rest. Basivenalia are fused to the veins of the vannal unit except of free JB in the fore wing of Cicadelloidea (Fig. 140). AP and JP in all hind wings are cut off their basivenalia by folds. Only in the fore wing of Cicadoidea a distinct brace from AA towards CuP is detectable (Fig. 98). The av passes immediately into the axillary cord at the hind border of the jugal lobe (Figs. 156, 159) or through AP in the fore wing (Figs. 70, 186).

Fore wing

AA is a single vein and AP bifurcates at about half of length of the inner margin (Figs. 11, 74, 115, 134) and fuses with J (Figs. 72, 73). In some Membracidae of Cicadelloidea and most Fulgoroidea both anal veins fuse subterminally forming Y-vein (Figs. 80, 135, 138). In many singing cicadas (Fig. 98), *Muiria* of Fulgoroidea (Fig. 53) and some Typhlocybinae of Cicadelloidea AP is single. Arrangement of the anal veins in relation to CuP is very diverse in Fulgoroidea (Figs. 48, 49, 73, 77, 78). The jugal vein has distinctly separate basal articulation (Figs. 71, 75, 99) and is folded under clavus (Figs. 72, 73, 100, 140). In some Cercopoidea (Fig. 118) there is a sclerotization on the jugal membrane. Jugal veins in some non flying wings are transformed into "tonguing and grooving" device coupling both wings together (Figs. 184, 185).

Hind wing

AA joins the composite sclerite Cu-JF ("3 Ax") through its basivenale while AP (–) de-pigmented and desclerotized basally leaves the same place of attachment slightly behind (Figs. 42, 71, 128). AP bifurcates near its base and its hind subbranch (AP″) crosses the anojugal fold joining JA. The fusion is almost complete, at least subasally, in all super-families (Figs. 14, 155, 168, 169) except Cercopoidea. In Cercopoidea (Figs. 127, 167) AP″ runs parallel to the atracheate and lumenless JA and in some Fulgoroidea it secondarily branches on the jugal lobe (Figs. 31, 44) or, at least, re-emerges (Fig. 14). The hind part of the jugal lobe of Flatidae (Fig. 34) bears additional channels. In Fulgoroidea AP′ usually branches (Figs. 15, 82) but it is single when venation in general is reduced (Figs. 61, 88 89) and still further reduced in non flying wings (Fig. 22). AA and AP′ coalesce on some distance subbasally and (except some Typhlocybinae) disjoin again in all Cicadelloidea (Figs. 159, 164), some Issidae (Fig. 17) and some Cercopoidea (Fig. 127). Cicadelloidea have no lumen in AP″+JA vein with the exception of Tartessini (which have also a marginal membrane behind av on the jugal lobe) (Fig. 156). JP is present everywhere as a rudiment accompanied by folds (Figs. 71, 128, 155 167–169) and often folding itself.

Discussion of the vannal unit — anojugal complex

Misinterpretations of the veins of this unit was caused by desclerotized and depigmented connection of AP with its basal articulation in the hind wing and too heavy sclerotization of the base of clavus to trace the basal attachment of AA in the fore wing (e. g. EMEL-JANOV, 1977).

In the present study homologization of the veins of anojugal complex is based on their basal connections. The minute sclerotization on the axillary membrane in the fore wing of some Cercopoidea (Fig. 118) is suspected of being a remnant of JP because of its position comparable to that of JP in the hind wing.

The invasion of the anal vein into the area of jugal membrane accompanied by expansion resulting in the jugal lobe in the hind wing is evident when to trace the tracheate and innervated AP" and sclerotized, pigmented, separately attached basally but devoid even the haemolymph channel JA (Figs. 44, 71, 76, 128). The marginal position of the av lends the additional support to the recognition the region in question as the jugal membrane. MARTYNOV (1924) called "neala" the fan-like expansion of the jugum (jugal membrane) in the hind wing. He has found "neala" as the evolutionary achievement of Neoptera and provided examples among other groups than Hemiptera, which had either primary, not expanded jugal veins (e. g. Trichoptera) or expanded AP on its own area while jugum itself reduced (Orthoptera). Although in all that MARTYNOV has erred, as it is seen in the material presented above, the idea itself (somewhat downplayed by WOOTTON, 1979) is unexpectably materialized in the wings of Auchenorrhyncha.

Remarks
The presented results are supposed to explain all the observed phenomena with the closest proximity to what really occurs. That justifies omitting from discussions the opinions that' have been held arbitrarily. The exception is HESLOP-HARRISON (1955a, b) whose papers have influenced European authors, and WOODWARD et al. (1970) because of the belief that "Insects of Australia" is the best handbook of entomology.

Summary
The paper contains results of the original studies of the representative sample of Auchenorrhyncha aimed at verification of the scheme of the flying wing introduced into the literature by KUKALOVA-PECK (1983). The following morpho-functional units are distinguished: pronating (Pc, CA, and CP, the last including ScA), axial (ScP, RA, and RP+MA), transitional (MP), plical (CuA and CuP) and vannal (AA, AP, JA und JP). Reasons for the presented homologies of the veins are discussed at the certain units.

Zusammenfassung

HAUPTADERN DER FLÜGEL DER AUCHENORRHYNCHA
(INSECTA, RHYNCHOTA: HEMELYTRATA)

Die Arbeit enthält die Resultate originaler Studien an einem repräsentativen Spektrum der Auchenorrhyncha, welche darauf gerichtet sind, das von KUKALOVA-PECK (1983) in die Literatur eingeführte Modell des flugfähigen Flügels zu verifizieren. Die folgenden morphologisch-funktionalen Einheiten werden unterschieden: pronale (Pc, CA und CP, letztere einschließlich ScA), axiale (ScP, RA und RP+MA), transitionale (MP), plikale (CuA und CuP) und vannale Einheit (AA, AP, JA und JP). Die Gründe für die aufgezeigten Homologien der Adern werden bei den jeweiligen Einheiten diskutiert.

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[3] Positions omitted from the list are to be found in KUKALOVA-PECK (1983) or/and in HAMILTON (1972a, b).