Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta)

FABIAN HAAS[1] AND JARMILA KUKALOVÁ-PECK[2]

[1] Section of Biosystematic Documentation, University of Ulm, Helmholtzstr. 20, D-89081 Ulm, Germany;
e-mail: fabian.haas@biologie.uni-ulm.de

[2] Department of Earth Sciences, Carleton University, Ottawa, ON K1S 5B6, Canada; e-mail: jkpeck@ccs.carleton.ca

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Abstract. The Dermaptera are a small order of insects, marked by reduced forewings, hindwings with a unique and complicated folding pattern, and by pincer-like cerci. Hindwing characters of 25 extant dermapteran species are documented. The highly derived hindwing venation and articulation is accurately homologized with the other pterygote orders for the first time. The hindwing base of Dermaptera contains phylogenetically informative characters. They are compared with their homologues in fossil dermapteran ancestors, and in Plecoptera, Orthoptera (Caelifera), Dictyoptera (Mantodea, Blattodea, Isoptera), Fulgoromorpha and Megaloptera. A fully homologized character matrix of the pterygote wing complex is offered for the first time. The wing venation of the Coleoptera is re-interpreted and slightly modified. The all-pterygote character analysis suggests the following relationships: Pterygota: Palaeoptera + Neoptera; Neoptera: [Pleconeoptera + Orthoneoptera] + [Blattoneoptera + (Hemineoptera + Endoneoptera)]. Blattoneoptera share at least 15 wing apomorphies with the sistergroup Hemineoptera + Endoneoptera and none with the Orthoneoptera and Pleconeoptera; Blattoneoptera: (Grylloblattodea + (Dermaptera + Dictyoptera)); Dictyoptera: (Mantodea + (Blattodea + Isoptera). Dermaptera share 13 wing apomorphies with the sistergroup Dictyoptera. In order to document the intra-ordinal relationships of Dermaptera, 18 new characters of venation and articulation are added to an existing data set and analyzed cladistically. The following relationships are suggested (43 characters, tree length 72, CI 0.819 and RI 0.935). Dermaptera: Karschiellidae + ("Diplatyidae" + ("Pygidicranidae" + (*Allostethus indicum* + (Anisolabididae + ("Labiduridae" + [Forficulidae + (Chelisochidae + Spongiphoridae)])))))). The taxa in quotation marks are probably paraphyletic. Fossil Dermaptera and "Protelytroptera" show that wing-folding characters were already present in Permian ancestors. The evolution of the dermapteran wing-folding mechanism is discussed and the hindwing is presented as a working "origami" model, which will fold as in living earwigs. The functional role of the wing base in wing folding is examined. Characters in orders and other higher taxa are not independent and cannot be analyzed out of context with their groundplans. Higher systematics is dealing with diametrally different problems than species-level systematics. The necessity of using a different methodology for species-level and higher-level phylogenetics is discussed and recommendations are made.

CONTENTS

INTRODUCTION

The Dermaptera (earwigs) are a small insect order containing about 2000 species (Sakai, 1996). The primary dermapteran characteristics are a unique folding of the hindwings, and the pincer-like cerci. The hindwings contain an enormous fan supported by anal branches, which

unlike other pterygote orders, radiate from the centre of the wing rather than from the wing base. The wing fan is folded twice transversely with a folding ratio of about 10 (Haas & Wootton, 1996), compared to 4 in Coleoptera (Haas, 1998). The wing articulation has a large membranous area in its centre, which in the other pterygote insects is used for transmitting major forces during flight. Furthermore, the hindwing is folded by intrinsic elasticity and uniquely unfolded with the help of the cerci (Kleinow, 1966; Haas et al., 2000; this paper).

The evolution and diversification of the hindwing formed a major set of characters, which show the phylogenetic relationships of Dermaptera and between the dermapteran families. The crucial requirement for using the wing complex in higher systematics is its accurate homologization at the levels of Pterygota, Palaeoptera, Neoptera, superorder and order. Idiosyncratic, "convenient" wing nomenclatures, which were developed through time for each pterygote order, have practical use for the lower taxa, but are useless for the inter-ordinal relationships. We employ an all-pterygote homologous nomenclature, and for Neoptera the reference scheme reconstructed by Kukalová-Peck (1983, 1985, 1991, 1997) and improved here (Fig. 1). The Dermaptera hindwing is now accurately homologized, newly interpreted and compared in detail with the plesiomorphic representatives of the monophyletic Dictyoptera (the Mantodea, Blattodea and Isoptera), which was found to be the sistergroup. The phylogenetic relationship of Blattoneoptera to Hemineoptera, Endoneoptera, Orthoneoptera and Pleconeoptera is examined and documented in the hindwings of plesiomorphic representatives. For the first time, the fully homologized characters of the pterygote wing complex are presented in a table, to provide a broad evolutionary setting and to offer a fast and concise overview of the many characters of the neopterous superordinal lines.

Our analysis of the hindwing character complex supports the sistergroup relationship between the Dermaptera and Dictyoptera with 13 characters, and provides the reasoning for the rejection of alternatives offered by other authors. We did not include Zoraptera in our analysis, because convincing wing characters are not yet available. For further discussion of Zoraptera see Boudreaux, 1979; Štys & Biliński, 1990; Kukalová-Peck & Peck, 1993; Kristensen, 1995; Rasnitsyn, 1998; and a critical review here.

By including fossil "Protelytroptera" and Dermaptera, we are able to support the hypothesis that the "Protelytroptera" are paraphyletic and that some of their representatives are indeed in the stem line of Dermaptera. The study of stem-line Dermaptera was found to be necessary for understanding the evolution of the autapomorphic hindwing folding in extant Dermaptera. Only with the clues from fossils was it possible to reconstruct the evolutionary steps between the cockroach-like hindwing (folding in a relatively simple way) and the highly derived modern dermapteran hindwing (folding in a very complex way).

Further diversification of the dermapteran wing complex enabled us to re-assess the intra-ordinal relationships of the Dermaptera. In contrast with previous studies (Giles, 1963; Popham, 1985) we found many differences among dermapteran families and recorded 18 new phylogenetically informative characters, thus almost doubling the existing data set of Haas (1995).

Morphological complexes and their functions are profoundly interwoven. Many wing character states described here cannot be interpreted without considering their function. They were examined with the help of paper models, which duplicate the natural movements of sclerites and fields during folding and unfolding. We offer figures of these models with folding instructions, which make it possible for an interested reader to repeat our experiments. Working paper models are the best way to demonstrate and learn the movements involved in the wing folding mechanism. They also reveal functional reasons for many unusual characters of Dermaptera, such as the large membranous area in the centre of the articulation. A paper model of the hindwing made to our instructions will fold and unfold with some help, the same way as do the hindwings of living earwigs.

MATERIALS AND METHODS

Nomenclature and homology

The neopterous wing characters analyzed here (Table 6) suggest a grouping of the related higher taxa (orders) into five superordinal lines. To avoid confusion, we follow the proposal of JKP (in Kukalová-Peck & Brauckmann, 1990) to use the prefixes of the traditional and generally known names, plecopteroids, orthopteroids, blattoids, hemipteroids, endopterygotes combined with the ending -neoptera, to identify the superordinal lines:

Pleconeoptera: Plecoptera, Embioptera.
Orthoneoptera: Ensifera, Caelifera, Phasmatodea.
Blattoneoptera: Grylloblattodea, Zoraptera?, Dermaptera, Mantodea, Isoptera, Blattodea.
Hemineoptera: Psocodea, Thysanoptera, Phthiraptera, Sternorrhyncha, Coleorrhyncha, Heteroptera, Fulgoromorpha, Cicadomorpha.
Endoneoptera: Hymenoptera, Coleoptera, Strepsiptera, Neuroptera, Megaloptera, Raphidioptera, Mecoptera, Diptera, Siphonaptera, Trichoptera, Lepidoptera.

The all-pterygote homologization of the wing structures was based on comparisons between many representatives of all pterygote orders, extant and extinct. The previously published hypothetical pterygote protowing (Kukalová-Peck, 1983, 1997; see characters listed in Table 6A) was recently found preserved in Palaeozoic fossils (JKP, unpublished observation). It is retained in the prothoracic wing of extinct Palaeodictyoptera and Geroptera (the most primitive extinct order of Odonatoptera) (Kukalová-Peck, 1978, Fig. 14; Wootton et al. 1998: 599; Wootton & Kukalová-Peck, 2000). The prothoracic wings in both orders are similar, in spite of the fact that they are distantly related and their wings and flight are highly dissimilar. Since the prothoracic wing pair was never involved in powered aerial flight, this similarity very probably indicates that both prothoracic wings are in a near original protowing condition. The stunning resemblance between the hypothetical protowing based on characters shared by all Pterygota and published in 1983, and the protowing-like prothoracic wings identified 15

years later in Carboniferous fossils, provides a proof, which is very significant for higher phylogenetics. Namely, that the morphological ground patterns, usually missing, can be reliably reconstructed based on existing material. The key issue here is that the study must be sufficiently broad. For a short review of protowing morphology, nomenclature and use in the relationship of orders see Table 6. We use the all-pterygote wing nomenclature developed by Kukalová-Peck (1983, 1985, 1991, 1997). The neopterous articular sclerites, unique folds, wing lobes, veinal stems and braces are presented in a special Neoptera reference scheme in Fig. 1.

Neopterous superorders and orders relate to each other in the similar transformations of their wing complexes. Typically in each order, several groups of wing characters show the same relationship (Table 6 B–H). Thus, true synapomorphies can be recognized by treating the wing complex in each order as a separate entity, and by always judging its characters in this mutual context (see examples in Table 6). This context is necessary to overcome rampant homoplasies. Most wing characters are extremely homoplasious in many unrelated higher taxa. When extracted from their special, integrated wing complexes and assessed as individual "neopterous" characters, most wing characters loose their phylogenetic information and instantly turn homoplasious. This explains why, in systematic practice, the direct application of a successful species-level methodology (no matter how sophisticated) to order-level phylogenetics, never worked in the past and never will in the future.

For determining derived character states we use the following criteria, verified by a century of studies of the wing structure in fossil and living insects.

(1) The pterygote principal veins and branches, once lost, do not reappear.
(2) The principal veins, once fused into veinal stems or one with another near the wing base, do not separate.
(3) The pterygote articular sclerites, once reduced, do not reappear.
(4) The articular sclerites, once fused, do not unfuse.

For an unreduced wing system and accurately homologized nomenclature in Neoptera, see the reference scheme in Fig. 1. For the arrangement and nomenclature of veins and folds in the Dermaptera hindwing see Fig. 2. The abbreviations used in the text and figures are given in Table 1.

A reviewer proposed to us that a distinction between a fold and a flexion line should be recognized. The distinction was introduced by Wootton (1979) to differentiate between folding lines, which are important for folding, and flexion lines, whose main function is in flight. We do agree with this distinction and see the usefulness of it. However, in order to keep our text and figures consistent, we here use claval fold instead of the more exact expression claval flexion line or claval furrow.

Techniques

To examine the wing venation and articulation, all specimens, either previously preserved in alcohol or pinned, were softened with hot water. After about 10 minutes they were soft enough to allow unfolding of the hindwings, which were not removed from the body. Wings were fixed on black foam using insect pins to prevent automatic folding of the wing. After drying they were examined using dissecting microscopes at magnifications of 10x to 70x. A camera lucida was used for drawings. It was not possible to present all parts of wings and wing articulations in exact proportions because of their irregular topography. In some cases, especially for the wing articulation, alcohol-preserved specimens with folded wings were used for the undistorted shape of the costal area and some articular sclerites.

Species examined

Original observations were made on the hindwing venation and articulation of the species listed in Table 2. The fossil taxa used are listed in Table 3.

Characters of extant Dermaptera taxa

Autapomorphies are known for only four out of nine "families" (Haas, 1995). We assume that the currently used "families" of the Dermaptera are monophyletic. The assumption of monophyly is a working hypothesis, which we followed in the present account as long as the character states within a "family" were homogeneous; otherwise the species were listed separately. Although many differences in wing articulation and venation are described below, not all of them are included in the phylogenetic analysis. Only those are used which appeared in clearly distinguishable character states, independent of body size and general sclerotization of the specimens.

Many Dermaptera are wingless, such as the Karschiellidae, and in some cases not all characters for winged species were available for our study because the specimens were previously damaged or a dissection was not allowed. The "collection dilemma" emerged, whether rare specimens should be kept intact for future generations, or examined and partially damaged. Fortunately for this paper, the policy of the Academy of Natural Sciences, Philadelphia was in favour of scientific advancement and dissection.

Apart from the venation and articulation characters described here, we include additional characters presented by Haas (1995). These characters from thorax, legs and genitalia were assessed with the available species. Only changes in characters used by Haas (1995), such as character states for specific taxa, are indicated. For a detailed discussion of these characters we refer to that publication. Three species of Blattodea (*Leucophaea maderae, Polyphaga aegyptiaca, Periplaneta americana*) are used as an outgroup. However, for many wing characters there is no suitable outgroup, because the dermapteran hindwings are unique in their structure. The character state distribution is listed in Table 4.

Characters of fossil Dermaptera taxa

Fossil Dermaptera are often grouped in the taxon "Archidermaptera". The relationships of fossils to extant Dermaptera is re-assessed, predominantly with body characters, because wing characters are almost never preserved. The characters of the fossil taxa (Table 5) have been extracted from the literature (Martynov, 1925; Tillyard, 1931; Carpenter, 1933, 1992; Carpenter & Kukalová, 1964; Jun-feng, 1994; Vishnyakova, 1980). It was not possible to re-assess the characters because the fossils themselves were not available to us. Therefore, the characters are not discussed and we follow the original descriptions. In cases when a fossil Dermaptera genus contains several species, only one representative species was selected to keep the number of taxa low for the computer analysis. The other species were not included. Only one species of extant Dermaptera, *Diplatys jacobsoni*, was included to reduce calculation time. *Periplaneta americana* was used for outgroup comparison. The character state distribution is listed in Table 5.

Analysis

The data sets for extant and fossil taxa are analysed separately because the wing venation and articulation, on which most characters in extant taxa are based, are not preserved in fossil Dermaptera and "Protelytroptera". A parsimony analysis for each data set was conducted with PAUP 3.1 (Swofford, 1993) using the "Heuristic Search Option" and assuming "Accelerated Transformation" (ACCTRAN). Multiple character states were uncertainties (not polytomies), and "Outgroup Rooting" was

TABLE 1. The following abbreviations are used in the text and the figures. Small initial letters indicate a cross vein, cross-vein associated structure, of fold.

Abbreviation	Full spelling
1, 2, 3, 4Ax	First, second, third, fourth axillary
AA, AP	Anal anterior, anal posterior
abr	Anal brace
af	Anal fold
ap3-ap4	Cross-vein between AP3 and AP4
ap4-ja1+2	Cross-vein between AP4 and JA1+2
AWP	Anterior wing process (PRSc + PRR)
AX, AXA, AXAJ	Axalare, anal axalare, anojugal axalare (3Ax saucer)
AXC, AXCu, AXJ	Costal axalare (convenient abbreviation for precosto-costal axalare AXPCC, used in this paper), cubital axalare (3Ax goblet and heel), jugal axalare
AXPCC	Precosto-costal axalare
AXM, AXR, AXSc,	Medial axalare, radial axalare, subcostal axalare
B, BA, BAA, BAA1+2, BAA3+4	Basivenale, anal basivenale, anal anterior basivenale, anal anterior 1+2 basivenale (anal brace), anal anterior 3+4 basivenale (articulation point between 3Ax anal arm and anal wing lobe)
BAP, BC, BCu	Anal posterior basivenale, costal basivenale (abbreviation for BPCC used in this paper), cubital basivenale
BJ, BM, BMA	Jugal basivenale, medial basivenale, medial anterior basivenale (a subdivision of medial basivenale)
BMP, BR, BSc	Medial posterior basivenale, radial basivenale, subcostal basivenale
BScA, BScP, BPCC	Subcostal anterior basivenale, subcostal posterior basivenale, precosto-costal basivenale (abbreviated as BC in this paper)
BT	Basitarsus
C, CA, CP	Costa, costa anterior, costa posterior
cf	Claval fold
clf	Concave longitudinal fold
Cu, CuA, CuP	Cubitus, cubitus anterior, cubitus posterior
CX	Coxa
exc1, exc2	Extension cross-vein 1, extension cross-vein 2
F, FA, FAJ, FC, FCu	Fulcalare, anal fulcalare (3Ax anal arm), anojugal fulcalare (3Ax anojugal arm), costal fulcalare (precosto-costal fulcalare, abbreviation for FPCC used in this paper), cubital fulcalare (3Ax cubital arm)
FJ, FM, FMCu, FPCC	Jugal fulcalare (3Ax jugal arm), medial fulcalare (part of medial plate), medio-cubital fulcalare (part of medial plate), precosto-costal fulcalare (abbreviated as FC in this paper)
FR, FSc	Radial fulcalare, subcostal fulcalare
FE	Femur
HP	Humeral plate (composed of FC + BC)
ib	Intercalary branch
J, JA, JP	Jugal, jugal anterior, jugal posterior
jbr	Jugal brace
lf	Longitudinal fold
M, MA, MP	Media, media anterior, media posterior
mf	Medial fold
mp-cua	Medio-cubital cross-vein, also brace or arculus in this paper
PAT	Patella
PC	Precosta or precostal strip
PFE	Pefemur
PR, PRA, PRC	Proxalare, anal proxalare, costal proxalare (abbreviation for PRPCC used in this paper)
PRCu, PRJ, PRM	Cubital proxalare, jugal proxalare, medial proxalare
PRR, PRSc, PRPCC	Radial proxalare, subcostal proxalare, precosto-costal proxalare (abbreviated as PRC in this paper)
PWP	Posterior wing process (PRA + PRJ fused with the tergum)
R, RA, RP	Radius, radius anterior, radius posterior

TABLE 1 (continued).

Abbreviation	Full spelling
rf, rbc	Ring fold, ring brace
rc, rfc	Ring cross-vein, ring fold cross-vein
Sc, ScA, ScP	Subcosta, subcosta anterior, subcosta posterior
SCX	Subcoxa (flattened into thoracic pleuron in pterygote thorax)
tf	Transverse fold
TI	Tibia

used. In phylogenetic reconstruction the characters are equally weighted, non-additively coded and not polarized. Character transformations were examined using MacClade 3.04 (Maddison & Maddison, 1992).

Movement of wing articulation

The articulation sclerites were observed during experimental promotion and unfolding of the wings in alcohol-preserved specimens of *Labidura riparia*, manipulating them under a dissecting microscope. The results were compared with those of Kleinow (1966) on *Forficula auricularia*.

RESULTS

Order Dermaptera Kirby, 1815.
Occurrence: Jurassic to Recent, worldwide.

Diagnosis of the hindwing

See characters in Table 6 and Figs 2–10, 18, 19. Characters of the higher taxa (order and up) are dealt with only at the ground pattern level. Character states below the order-level are irrelevant for the phylogenetic position of Dermaptera. Only the characters of dermapteran families are included. Dictyoptera, whose wing complex is closely related to Dermaptera, are treated here as the sistergroup. Zoraptera, which may be related to Dictyoptera, have petiolate wings and their wing articulation is not known; they could not be included into this analysis (see "Discussion").

The hindwings of Dermaptera differ from those of the sistergroup Dictyoptera (Mantodea + (Blattodea + Isoptera)) (Table 6E) mainly in the character states accommodating the quadruple wing folding. This adaptation includes a very narrow remigium with condensed and simplified radial and medial sectors; anojugal lobe exceptionally enlarged and supported by AP branches radiating from its centre; arculus (mp-cua) present in both wing pairs; and AA1+2 absent. The wing articulation differs in PRR fused with 1Ax tail; 2Ax body reduced to a thickened proximal margin; 3Ax goblet and saucer long, slender and disconnected; 3Ax anal and jugal arm fused into a large, posteriorly extended anojugal arm; medial plate desclerotized; BSc very long, thin in the middle, pliable; BM proximally membranized; anojugal basivenalia fused into a plate; and, in a unique anal brace overriding the cubital basivenale (see below).

Dermaptera share with their sistergroup Dictyoptera a distinctive, very complex flight apparatus (see Table 6 E). This includes wing position, shape and lobes, flight musculature, and fusions, reductions and braces in the wing venation and articulation. This flight apparatusbelongs to the ground pattern of these taxa and is phylogenetically informative (Figs 1, 4–13, 20–22; see discussion below). Please note that individual characters usually make sense only if used within the context of their own order; if extracted from the order and compared anonymously as neopterous characters, they would turn homoplasious and uninformative.

The basal flight adaptations in Dermaptera and Dictyoptera are related to those of Hemineoptera + Endoneoptera (Figs 16, 17; Table 6, clade 5). In contrast, Pleconeoptera + Orthoneoptera (Figs 14, 15, 21, 22) (Table 6, clade 2) have a very different flight-generating system and probably represent the sistergroup of Blattoneoptera + (Hemineoptera + Endoneoptera). Note that the same deep split is repeated in the construction of the third ovipositor valve (Sharov, 1969, Fig. 77, 78; Hennig, 1981). The Dermaptera hindwing characters are offered in Table 6, documented in Figs 2, 4–10, and discussed in more detail in a separate section below.

Description of the hindwing

For plesiomorphic character states at the Neoptera level see the reference scheme in Fig. 1. For character coding: 0 plesiomorphic; 1, 2, 3 apomorphic, unordered, see Table 6. The ancestral character states of Dermaptera are best preserved in *Apachelytron transversum*, Lower Permian, Czech Republic (Fig. 3), which we consider to be a representative of the extinct dermapteran stem group and close to the stem line.

Fustis. The fustis (Latin: club-shaped) is a unique, distinctive, sclerotized part of the dermapteran remigium delimited anteriorly by RA, distally by the apical margin of the ancestral remigium and by the transverse fold, and posteriorly by CuA and CuA1+2 (Figs 2, 4). The fustis is divided into **base** and **head**, and bisected by a **groove** in Spongiphoridae, Chelisochidae and Forficulidae (Fig. 4). The head is the visible part of the fustis when the hind wing is at rest and covered by the tegmen. The groove in the fustis marks the posterior margin of the tegmen and seemingly gives the wing package additional flexibility to follow the movements of the abdomen. The fustis often contains variously long RP, MA and a strong MP, and a broad to very broad CuA1+2.

Stem line homologue. The portion of the wing in *Apachelytron transversum*, which evolved into the fustis in extant Dermaptera, is marked by striation (Fig. 3).

Precostal strip (PC). The precostal strip is broadened anteriorly into a soft flap in Apachyidae, Anisolabididae, "Labiduridae", Forficulidae, Chelisochidae and Spongiphoridae (Fig. 4).

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Sistergroup homologue. In Dictyoptera, the precostal strip is not broadened, but is incorporated into the costal margin (Figs 11–13).

Comments. In Hemineoptera + Endoneoptera (Figs 16, 17), the precostal strip is in many forewings of Hemiptera and Endoneoptera broadened ventrally (Coleoptera); in the hindwings, it is sometimes broadened anteriorly into a membranous lobe similar to that in Dermaptera (Kukalová-Peck & Lawrence, 1993). In contrast, Pleconeoptera + Orthoneoptera (Figs 14, 15) have the precostal strip fused with the costa (C) in a uniform, not broadened costal margin.

Costal margin (C, CA + CP), outer apical area. The costal margin is unique, pliable, running to the end of the fustis. Apical area is a small, triangular area immediately distal to the fustis (Figs 2, 7–10).

Stem line and sistergroup homologue. In *Apachelytron transversm*, the costal margin is not pliable. The margin of the outer apical area beyond the fustis in Dermaptera (Fig. 2) belongs to an area between the anal fold and AP (Fig. 3). In Dictyoptera, the costal margin is also firm, not pliable.

Comments. In the forewing of Hemineoptera and Endoneoptera, CA and CP run parallel to each other (in some fossil and modern Hemiptera and in the elytra of the primitive Coleoptera: Kukalová-Peck, 1991). In the hindwing, CA + CP form a well sclerotized costal margin. Costal margin also occurs in both wing pairs of Pleco-

Taxon / Character	0 123456789	1 0123456789	2 0123456789	3 0123456789	4 0123
Blattodea					
Leucophaea maderae	?????????	??????????	?10??00000	0000000101	0???
Periplaneta americana	?????????	??????????	?10??00000	0001000101	0???
Polyphaga aegyptiaca	?????????	??????????	?10??00000	0000000101	0???
Dermaptera					
Karschiellidae	?????????	??????????	?????00000	0000100111	1300
"Diplatyidae"					
Diplatys jacobsoni	000000000	0100000000	0100011110	0000100111	1020
Diplatys gerstaeckeri	000000000	0100000000	0000011110	0000100111	1020
Haplodiplatys bhowmiki	000000000	0100000000	0100001100	0000100111	1020
Haplodiplatys severus	000000000	0100000000	0100001100	0000100111	1020
"Pygidicranidae"					
Echinosoma micropteryx	100110000	0100000100	0100111110	0000100011	1010
Pyragra fuscata	100110000	0100000100	0100111110	0000100011	1020
Tagalina burri	100110000	0101100100	0100111110	0000100011	1010
Apachyidae					
Apachyus feae	110202100	1101111101	1010111110	0010101010	1111
"Labiduridae"					
Allostethus indicum	110211200	0100000100	0010111110	0011100010	1111
Forcipula clavata	110221210	1000111111	1010111110	0011100010	1111
Labidura riparia	110221210	1000111111	1010111110	0011100010	1111
Nala lividipes	110221210	1000111111	1010111110	0011100010	1111
Anisolabididae					
Carcinophora americana	110210200	1110111111	1010111110	0011100010	1110
Spongiphoridae	121231031	2011121111	1011111111	1111100010	1200
Chelisochidae	121231031	2011121111	1011111111	1111110010	1201
Forficulidae	121221021	1011121111	1011111111	1111120010	1201

Taxon/Character	4 456789	5 01234
Extant Blattodea		
Periplaneta americana	000000	00010
Fossil "Protelytroptera"		
Acosmelytron delicatum	011000	010?0
Apachelytron transversum	???000	0?010
Protelytron permianum	???001	1????
Extant Dermaptera		
Diplatys jacobsoni	111112	11213
Fossil Dermaptera		
Archaeosoma serratum	011012	11??3
Archidermapteron martynovi	011102	11001
Asiodiplatys speciosus	011102	11001
Dermapteron incertae	011002	11012
Longiceratus mesozoica	011002	11??1
Microdiplatys campodeiformis	011102	11001
Protodiplatys fortis	011102	11001
Semenoviola obliquotruncata	011012	11113
Semenovioloides capitatus	011012	11113
Turanoderma sepultum	011012	11113
Turanovia incompleta	011002	11012

neoptera + Orthoneoptera. In Orthoneoptera forewings, costa is desclerotized and pliable basally under the prothoracic shield. The long, branched ScA is supporting the anterior wing margin instead of costa (C). Therefore, the term "precostal area" in Orthoptera is erroneous. The area between the pliable costa and ScA is the costal area.

Subcostal basivenale (BSc). This sclerite is uniquely shaped. Proximally it is strongly sclerotized, protruding, consisting of BScA and BScP primitively separated by a suture. BScA is narrow and pointed, BScP is broad and lobate, articulated in-between the prongs of 1Ax head. The bulky proximal portion of BSc slims abruptly distally into a narrow and flexible "neck" (Figs 7–10).

Subcosta anterior (ScA). This sector forms a convex, blunt ridge, which creates a unique, long overhang hiding the ScP groove. The overhang occasionally contains remnants of ScA (Figs 7A, 8A, B).

Stem line and sistergroup homologue. ScA forms a short, oblique, blunt ridge running between BSc and the anterior margin in *Apachelytron transversum*. The blunt ScA ridge occurs also in Dictyoptera (in Blattodea + Isoptera and in blattoid stem line; it is broadened into a bulge in Mantodea) (Figs 3, 11–13).

Comments. In Hemineoptera + Endoneoptera the blunt ridge of ScA (noticeable especially in the forewings) extends into a broad, oblique bulge. In Hemineoptera, the
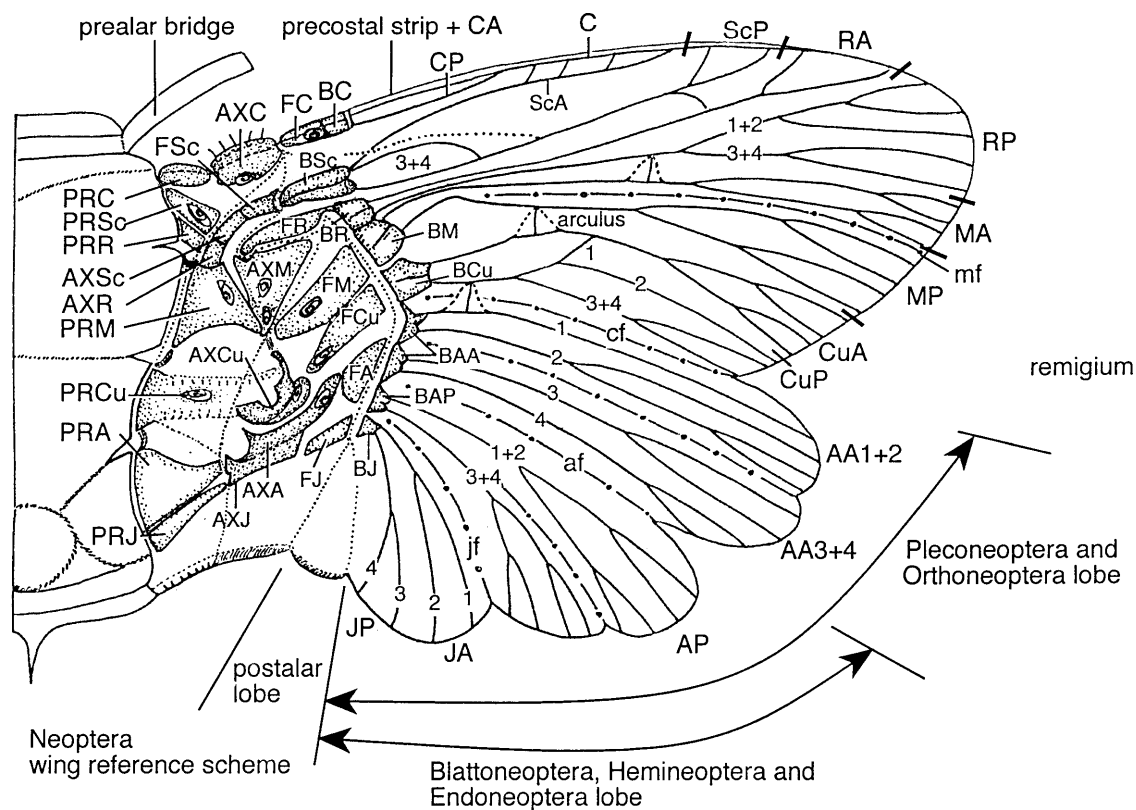
Fig. 1. A – Reference scheme showing the basal character states in the wing complex at the Neoptera level, with emphasis on the hindwings; loci of folds and of future fusions and braces in venation are indicated (Kukalová-Peck, 1997). Neoptera developed several styles of flight, each generated by a unique combination of different shape and size of wing pairs, wing lobes, flexion lines and folds, veinal fusions, braces, reductions, enrichments, and by various fusions, reductions and extensions of articular sclerites (see Table 6). Only the ground pattern level characters in each higher taxon are relevant in phylogenetics, but they are sometimes obscured by younger modifications and must be detected. They are more often found in basal representatives, but may occur in some derived phenotypes. Only a very broad study of the entire higher taxon, and its prospective relatives, brings reliable results.

bulge is weak or absent. In Endoneoptera the bulge is sclerotized, large, and flanked posteriorly by a prominent brace called **humeral vein**. In contrast, Pleconeoptera + Orthoneoptera have a primitive, vein-like ScA. In Orthoneoptera, ScA is very long with many branches and it supports basally the costal margin instead of the soft, pliable costa (Fig. 15). In Pleconeoptera, ScA is expressed in the plecopteroid stem line, but is short and inconspicuous in modern Plecoptera (Fig. 14) and Embioptera (JKP, unpublished observation).

Subcosta posterior (ScP). This sector is absent. Only a short, deeply incised groove runs parallel with R and RA and ends in the membrane beyond the middle of the fustis (Fig. 7A, B).

Stem line and sistergroup homologue. *Apachelytron transversum* has only slightly shortened ScP (Fig. 3). In ground pattern of Dictyoptera, ScP is relatively long (as in extant Mantodea; ScP is shortened in the blattoid stem line and very short in extant Blattodea + Isoptera; Figs 11–13).

Costal area (marginal area). In Dermaptera, the costal area (narrow area between the costal margin and subcosta) is unique in being soft and pliable (Figs 7–10).

Stem line and sistergroup homologue. The costal area in *Apachelytron transversum* is well sclerotized (Fig. 3). In Dictyoptera, Pleconeoptera and Orthoneoptera, it is also well sclerotized (Figs 11–15).

Radial basivenale (BR). In Dermaptera, this sclerite is uniquely shaped, divided by an embayment into a shorter proximal part, and an unusually long and swollen distal part. The latter is fused with the medial basivenale (BM), from which it is separated by a deeply incised groove. The proximal part of BR articulates with 2Ax, and the distal part gives rise to the stem of radius (R).

Sistergroup homologue. In Dictyoptera, BR is also immediately followed by the swollen radius (Figs 7, 11–13).

Comments. In Hemineoptera + Endoneoptera BR is followed by the thick base of radius, as in Blattoneoptera. In contrast, in Pleconeoptera + Orthoneoptera the base of radius is relatively slender and more even (Figs 14–15).

Radial sectors RA, RP, radial stem R. Sectors RA and RP form an extremely short stem of R (Fig. 7A). RA is swollen basally and forms the anterior margin of the fustis (Fig. 4). RP separates from RA at the sclerotized base of the fustis and ends within the sclerotized head of the fustis. RP is simple, accompanied by an adjacent MA,
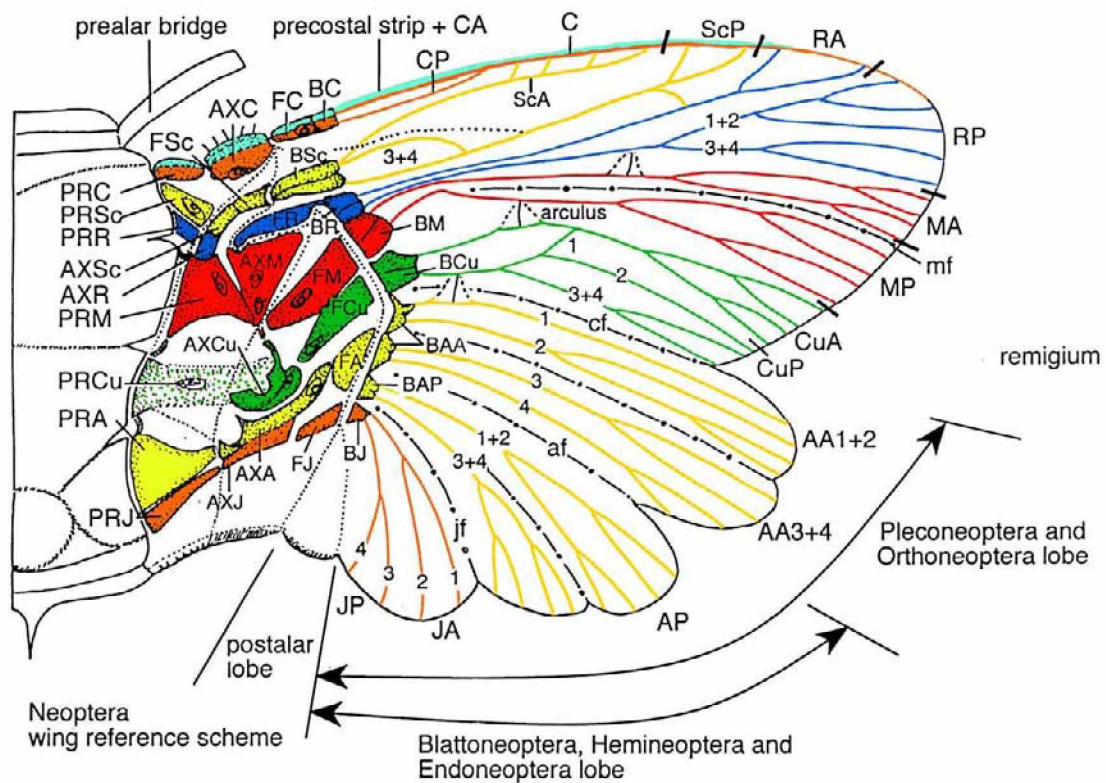
Fig. 1. B – Neopterous reference scheme: Articular sclerites; arrangement in **rows** aligned with wing veins is color-coded. Rows in Neoptera are partly irregular but the homologous rows in Palaeoptera are regular (Kukalová-Peck, 1983, 1997).
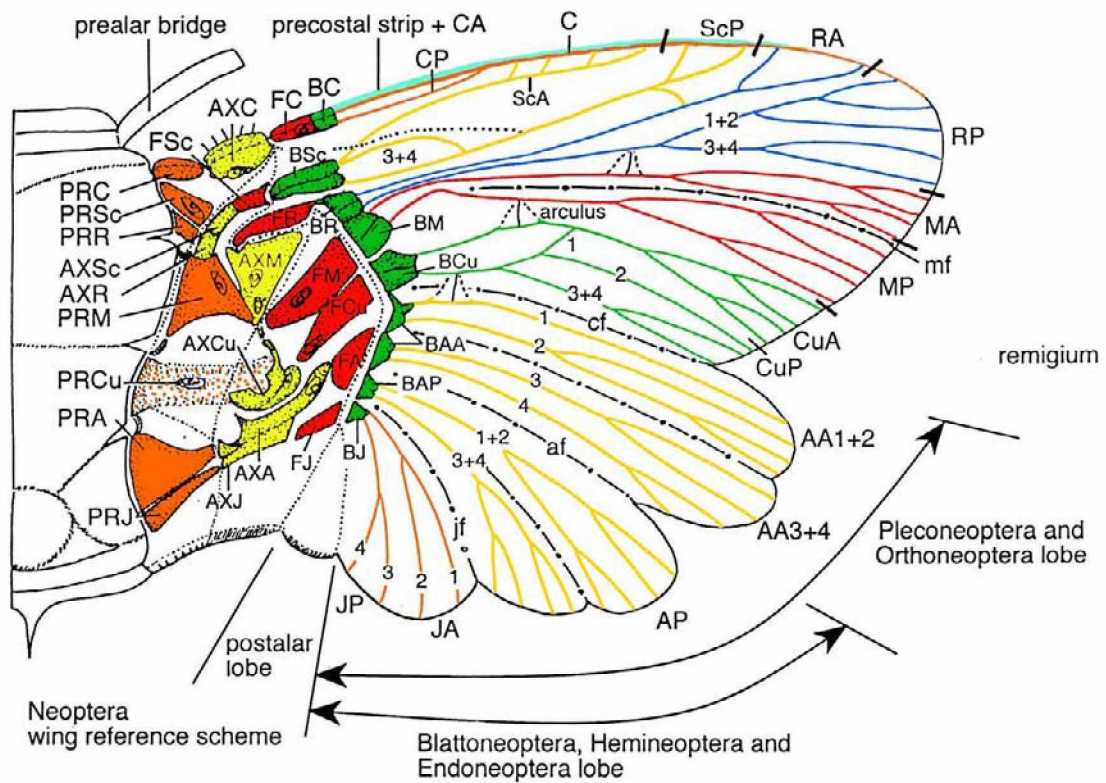
Fig. 1. C – Neopterous reference scheme: Articular sclerites; arrangement in **columns** is color-coded. Columns in Neoptera are partly irregular but the homologous columns in Palaeoptera are regular (Kukalová-Peck, 1983, 1997).

which soon separates and runs close and in parallel to RP (Figs 4D–G).

Stem line and sistergroup homologue. The stem of R (i.e. RA + RP fused) in *Apachelytron transversum* is much longer than in Dermaptera (Fig. 3). The stem of R in ground pattern of Dictyoptera is extremely short (as in extant Isoptera; R is somewhat longer in the blattoid stem line, Blattodea and Mantodea) (Figs 11–13; note that the base of RP in Isoptera is crossed by a fold and destroyed).

Comments. In the hemipteroid stem line the stem of R is absent in some species (Kukalová-Peck & Brauckmann, 1992; Figs 30–35). In modern Hemineoptera, R is relatively long. In Endoneoptera the stem of R is extremely short only in Coleoptera + Strepsiptera (JKP, personal observation); R is longer in neuropteroids (Fig. 17) and mecopteroids as well as in Hymenoptera (Kukalová-Peck, 1991). In the plecopteroid stem line (Paraplecoptera), the stem of R is absent in some specimens (a plesiomorphy at the Neoptera and Pterygota level); in extant Plecoptera, the stem of R is present but relatively short (Fig. 14). In Orthoneoptera, the stem of R is always well developed and strong (Fig. 15).

Medial basivenale (BM). In Dermaptera, this uniquely derived sclerite forms a long triangle with a broad proximal base. The proximal part of BM between the proximal part of BR and BCu is bent ventrally and membranised, thus giving more space to the complex movements of the wing articulation during wing folding. The distal part of BM is fused with BR and crossed by an oblique furrow. BM narrows rapidly apically in all families except in "Diplatyidae" (Figs 4A, 7–10).

Sistergroup homologue. In Dictyoptera, BM is associated with BR proximally and separated from it distally by a furrow (flexion line). The basal part of MP running very close to R and RP (largely retained in Mantodea, Fig. 13) is completely obliterated in Isoptera and in Blattodea (Figs 11–12).

Comments. In Hemineoptera + Endoneoptera (Figs 16, 17) the furrow that obliterates the base of MP in Blattodea is absent. BM is robust and associated with BR, with one significant exception. In Endoneoptera: Coleoptera + Strepsiptera, the radial and medial loop (engaged in folding and pulling the wing apex under the elytra) fall apart at base, one anteriorly, the other one posteriorly, to initiate folding. Consequently, BR and BM are separated by a unique, wide gap (this apex-folding mechanism in parasitic Strepsiptera has decayed, but its presence is still apparent and shown in several characters (Kukalová-Peck & Lawrence, 1993; Kukalová-Peck, 1997).

Media anterior (MA). In Dermaptera, the anterior medial sector (MA) fuses immediately at base with the extremely short R and RP in the sclerotized base of fustis. RP + MA are visible as a separate vein and the separation of MA from RP is weakly indicated (Figs 7A, 8B, C, 9A, B). The stem of M is absent.

Stem line and sistergroup homologue. In *Apachelytron transversum*, MA separates from RP near apex (Fig. 3). In Dictyoptera, MA fuses basally with R, but the entry is inconspicuous because disrupted by the fold between BR

and BM. The entry of MA is traceable and verifiable in serial dissection (K.D. Klass & JKP, personal observation). MA eventually separates from RP (but, this separation is often inconspicuous or reduced; Figs 11–13). In all Blattoneoptera the stem of M is always absent.

Comments. In Hemineoptera + Endoneoptera the stem of M is also always absent. The entry of MA into R (an important synapomorphy shared with Blattoneoptera) is quite inconspicuous, and the separation of MA from RP is vaguely noticeable only in plesiomorphic members. In contrast, Pleconeoptera + Orthoneoptera always bear the stem of M which forks clearly into MA and MP. This important stem of M is probably a synapomorphy.

Media posterior (MP). The MP is a strong, straight vein, which is uniquely unbranched and ending near the postero-distal end of the fustis (Figs 4D, F).

Stem line and sistergroup homologue. MP in *Apachelytron transversum* is strong, directed obliquely and posteriorly towards the end of the apical margin, and it bears a small terminal fork close to the anal fold (Fig. 3). This marks this location as the equivalent of the postero-distal end of the fustis in Dermaptera. In Dictyoptera, MP base is separated from BM by a fold (in Isoptera by a narrow fold; in Blattodea by a broad desclerotization; in Mantodea by a narrow, oblique fold) (Figs 1, 11–13).

Comments. MP base is present in Hemineoptera + Endoneoptera in basal members (Figs 16–17). There has been a long-lasting confusion about the interpretation of media in the neopterous orders, caused by a consistently incomplete preservation of MA and MP basally. The widespread misinterpretation of M, MA and MP (which show the basal split in Neoptera superordinal lines) literally prevented the use of the wing venation in higher phylogenetics. Homologization revealed that Blattoneoptera + (Hemineoptera + Endoneoptera) lack the stem of M, and Pleconeoptera + Orthoneoptera share the stem of M (Kukalová-Peck, 1991, 1997; Kukalová-Peck & Brauckmann, 1992) (Fig. 22; Table 3).

Medio-cubital brace (mp-cua, cross-vein or short fusion), the arculus. This flight-important brace occurs repeatedly in many taxa at many levels, as well as in both fore- and hindwing in Dermaptera.

Stem line and sistergoup homologue. Arculus occurs in *Apachelytron permianum* in both pairs of wings probably as a synapomorphy with Dermaptera. In the blattoid stem line, arculus is absent in both wing pairs (Fig. 20; Table 6D, G). In ground pattern of Dictyoptera, arculus is also absent in both wing pairs (in fossil stem line Dictyoptera and Isoptera only; in Blattodea and again in Mantodea, it is absent in forewings, but present in hindwings) (Figs 3, 7–13; Table 6G).

Comments. In Hemineoptera + Endoneoptera (Figs 16, 17) mp-cua brace is always present, as a synapomorphy. Arculus is clearly absent in protowing. The strong evidence for this assumption is that it is absent in the Blattoneoptera ground pattern, in the plecopteroid stem line (Paraplecoptera, Liomopteridae: Kukalová, 1964a; Carpenter, 1992, his Figs 63, 64), and in the Palaeoptera ground pattern (in Palaeodictyoptera: Kukalová-Peck,

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squama   ulnar area

costal area   fustis
outer apical area
inner apical area

claval fold

JP1+2

jugal cell

anojugal cell

AP4

Dermaptera folds and areas

AP3

broadening   ring fold

radiating fold
radiating branch
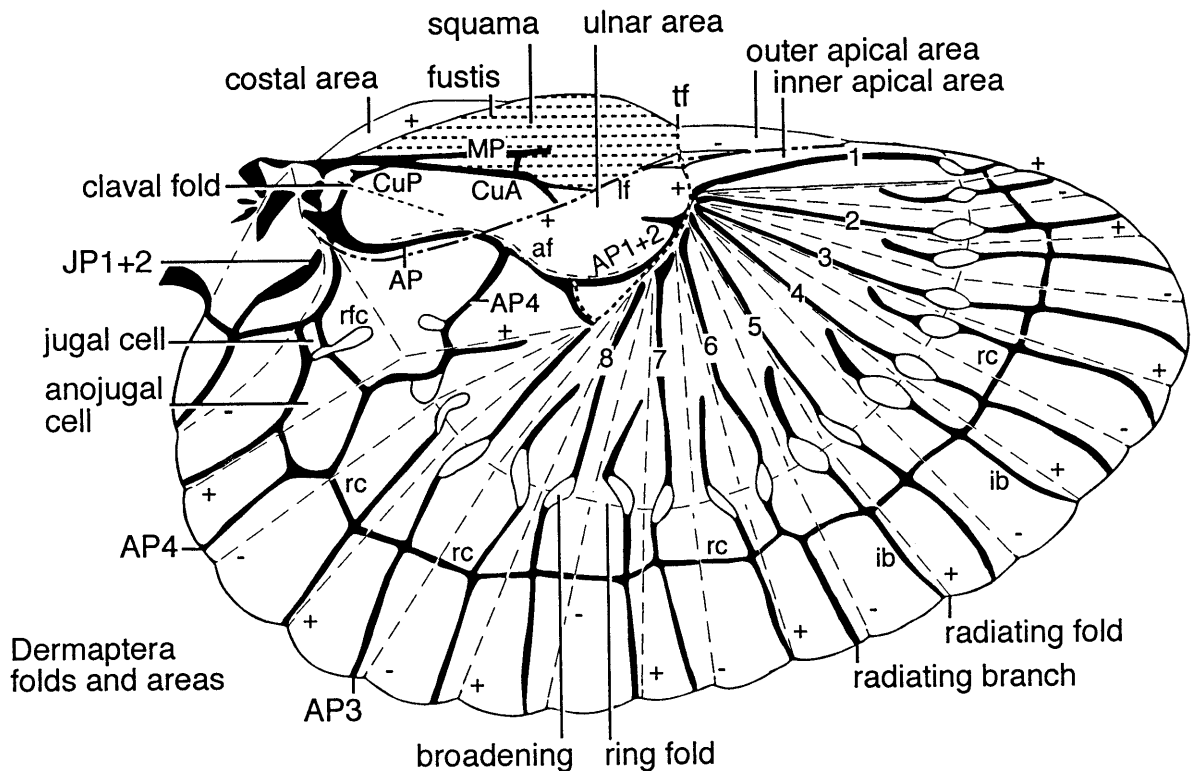
Fig. 2. Hind wing of *Forficula auricularia* showing veins, areas and folds. From Haas (1995) after Kleinow (1966).

1991). But, the arculus is present in modern Plecoptera, as an autapomorphy, and it is especially strongly expressed in Orthoneoptera, which share a very long fusion between CuA and M&MP (CuA fuses with M at base and separates from MP apically) (Figs 14–15; Table 6B, C).

Cubital basivenale (BCu). Dermapteran BCu is isolated from the combined basivenalia BR + BM by an extensive proximal desclerotization of BM (Figs 7–10). BCu is narrow, more or less desclerotized, and its distal end tapers into an empty groove. Consequently, the anal basivenale (BA), acting as an anal brace, overrides the groove and articulates directly with BM (instead of with BCu) (Fig. 25).

Sistergroup homologue. In ground pattern of Dictyoptera, BCu is also separated from the associated basivenalia BR + BM (only in Mantodea; in Blattodea + Isoptera, BCu is broadly fused with BR + BM) (Figs 11–13).

Comments. In Hemineoptera + Endoneoptera BCu is separated from BR + BM by a gap. In Pleconeoptera + Orthoneoptera, BCu is also separated from BR + BM (Fig. 14; Caelifera do not show this plesiomorphic character state: Fig. 15). As a plesiomorphy, basivenalia are hinged rather than fused. Fusions occur repeatedly, and provide informative characters at the order, family and subfamily level.

The stem of Cu. Dermapteran Cubital stem is proximally membranized and pointed into a short, massive spike (Figs 7–10).

Stem line and sistergroup homologue. In *Apachelytron transversum*, the stem of Cu is longer than in Dermaptera

and not pointed (Fig. 3). In ground pattern of Dictyoptera, the stem of Cu is very short (visible only in Mantodea; in Blattodea and Isoptera, the length of Cu is obscured because CuP is lost) (Figs 11–13).

Comments. In Endoneoptera + Hemineoptera, the stem of Cu is always present, extremely short in Hemineoptera, and significantly longer in Endoneoptera as an autapomorphy. In Pleconeoptera, the stem of Cu is short. Cu is totally absent in Orthoneoptera (in all representatives, extinct and extant). This absence of the basal fusion between CuA and CuP into a stem is a plesiomorphy at the protowing (Pterygota), Neoptera, and Orthoneoptera level (Fig. 15; Table 6A, C).

Emendation. The stem of Cu in Coleoptera was erroneously interpreted as "CuA", by Kukalová-Peck & Lawrence (1993) (see the footnote to Table 6H). Only after this mistake was emended do Endoneoptera show the important basal split into Hymenoptera and ((coleopteroids + neuropteroids) + mecopteroids) (JKP, own observation, Table 6).

Cubitus anterior (CuA). The CuA runs close to MP and forks at about the middle of the fustis into CuA1+2 and CuA3+4 (Fig. 4). CuA and CuA1+2 form the posterior margin of the fustis. CuA3+4 divides into a broad fork, which ends uniquely on the anal sector AP, rather than at the posterior wing margin.

Stem line and sistergroup homologue. In *Apachelytron transversum*, CuA bears pectinate branches, but they end similar as in Dermaptera, at the anal branch AA4 rather than at the wing margin. In the blattoid stem line and Dictyoptera, CuA is dichotomously branched and ends on the

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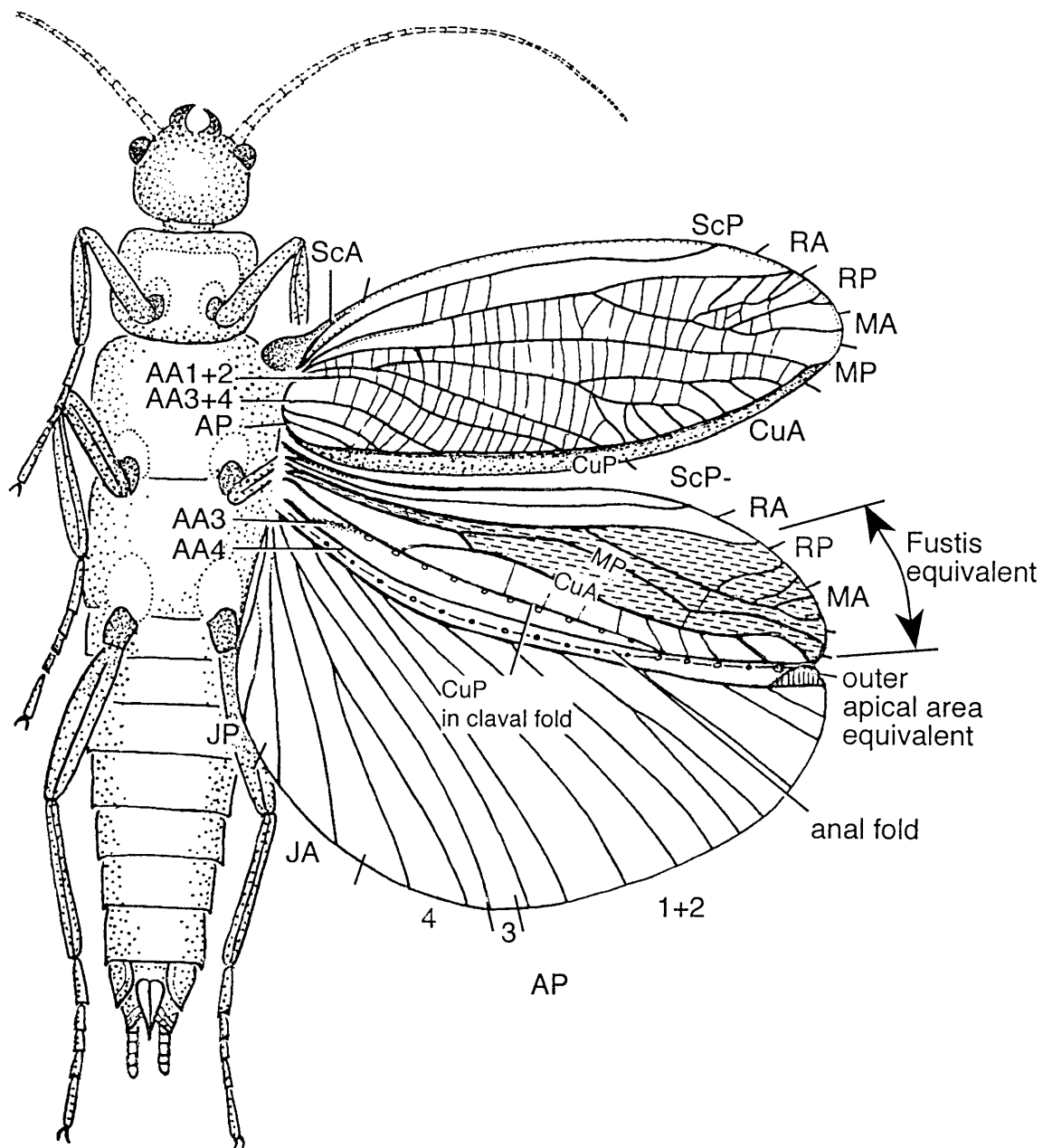
Fig. 3. Representative of dermapteran stem line, *Apachelytron transversum* from the Lower Permian of Moravia, Czech Republic. All dermapteran veinal fusions, braces, reductions and fold arrangements are present, but their expression is plesiomorphic. Left tegmen: Length 6 mm, width 2.2 mm. After Kukalová-Peck (1991), veinal interpretation revised.

posterior margin as in the other superordinal lines (Figs 11, 20, 21).

Cubitus posterior (CuP). The base of CuP is unique, strong, perpendicular to CuA, arched or almost straight, ending at the claval fold, and functioning as a strut (Figs 7–10). The rest of CuP is short, not reaching the wing margin; it may be replaced by a weakly sclerotized strip flanking the claval fold and ending near AP, or absent (Figs 7–10).

Stem line and sistergroup homologue. In *Apachelytron transversum*, CuP is also weak and ending on AA4 far from the wing margin, but it is somewhat longer than in Dermaptera (Fig. 3). In ground pattern of Dictyoptera,

CuP is very weak (as in extant Mantodea, CuP runs at the bottom of claval fold; CuP is absent in Blattodea + Isoptera) (Figs 11–13). In blattoid stem line (Fig. 20), the presence of CuP at the bottom of claval fold is possible but in a fossilized insect it cannot be securely confirmed. In Blattodea, the weak vein proximal from claval fold (Fig. 11B), which sometimes descends into the fold, starts from the BAA blood sinus. Therefore, it is positively AA1+2 and it can never be "CuP". Blood sinuses and their veins (veinal blood canals) are a single, continuous structure supplying blood.

Comments. In Hemineoptera + Endoneoptera and in Pleconeoptera + Orthoneoptera, CuP runs proximally from claval fold. In Orthoneoptera, CuP is richly dichoto-
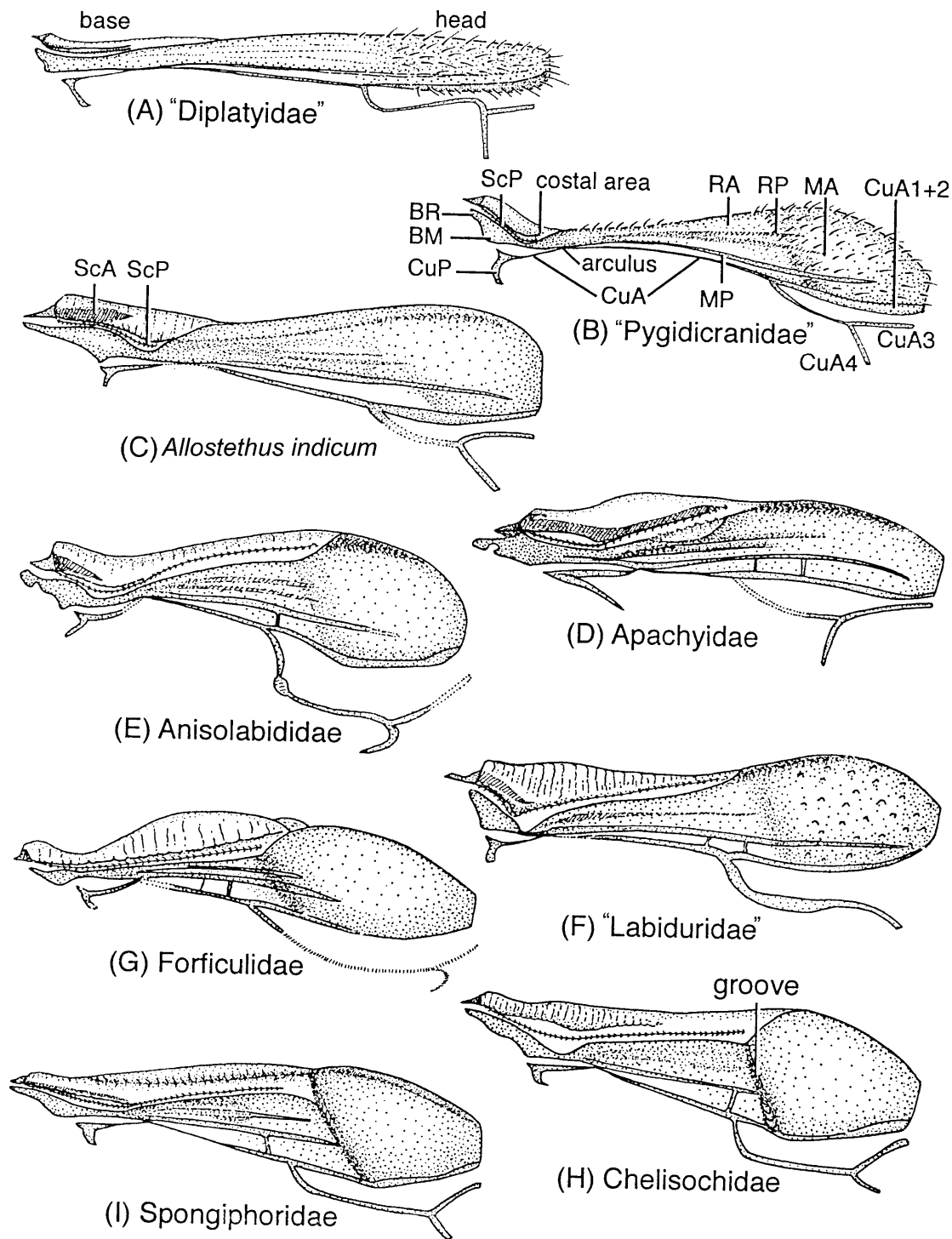
Fig. 4. Dermapteran fustis. A – the fustis, base and head; B – the remnants of principal veins. In Eudermaptera (G, H, I) the head is separated from the base by a groove.

mously branched, especially in the forewing (Table 6C). Note that a richly branched CuP also occurs in the hemipteroid stem line (in so called "Protorthoptera": Kukalová-Peck & Brauckmann, 1992) and in modern Hemiptera: Fulgoromorpha (Fig. 16; note that CuP forks distally beyond the figured part). CuP lost its branches independently many times.

Anal basivenale (BA), subdivisions BAA1+2, BAA3+4, BAP; and jugal basivenale (BJ). The dermapteran BA subdivision BAA1+2, BAA3+4, BAP and BJ are uniquely fused, consolidated into a single basivenal plate, and separated by sutures. BAA1+2 is a large, triangular sclerite with a shallow anterior embayment. BAA1+2 is almost seamlessly fused with a narrow BAA3+4. BAP and BJ are fused one to another and sepa-
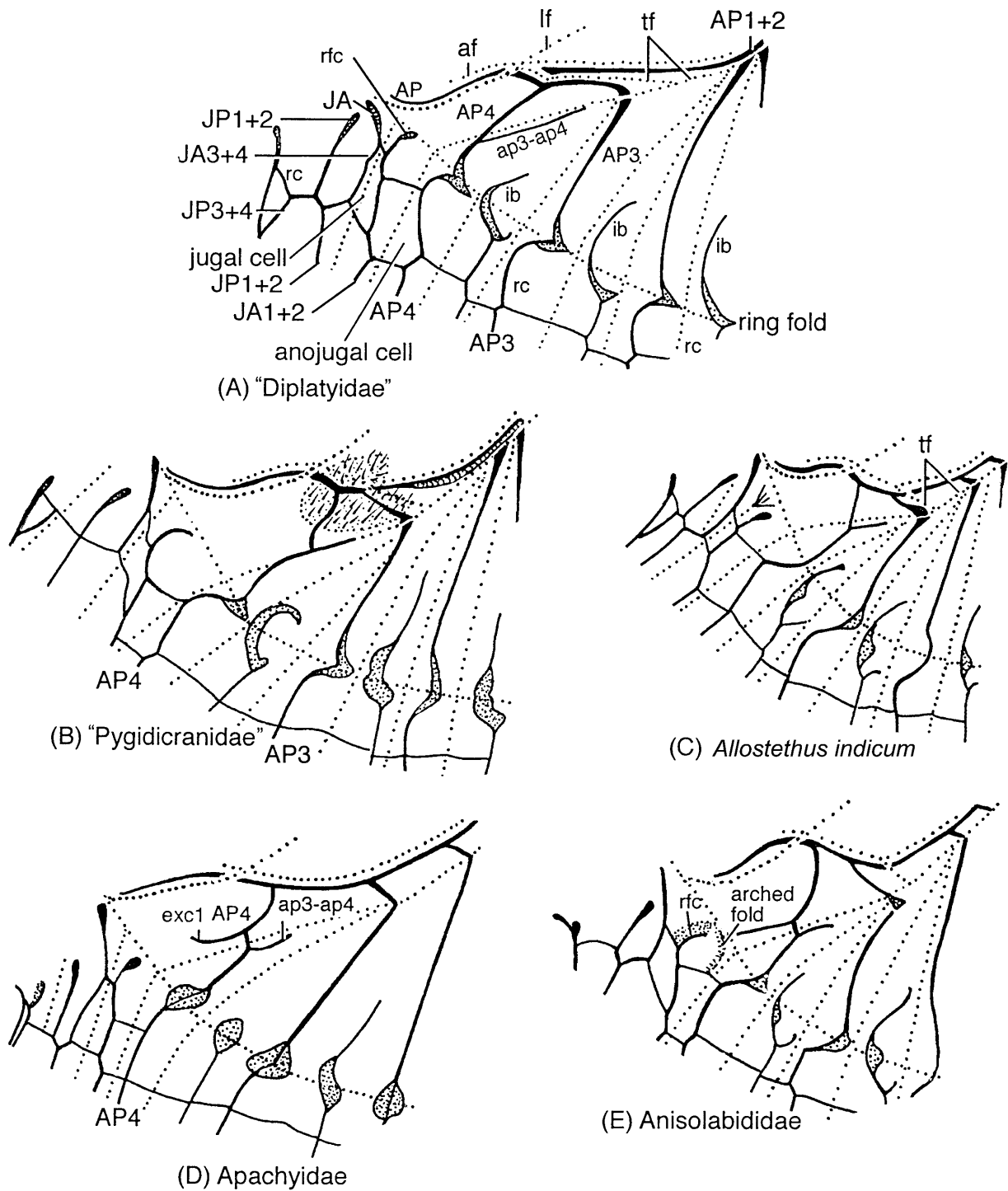
Fig. 5. Dermapteran anojugal lobe: The modifications in veinal support are characteristic for the different taxa. Veinal support fully homologized at the Neoptera level (5A).

rated by a deeply incised furrow from BAA3+4 (Fig. 7A). The boundary between BAP and BJ is either barely noticeable or protruding. In "Diplatyidae", BAP is only slightly curved in the middle and BJ is sloped ventrally (Fig. 7A). In *Echinosoma micropteryx* both BAP and BJ are curved and separated by a protruding suture (Fig. 7C). In all other examined species, BJ is curved and twisted (Figs 8–10). BJ articulates with the arm of 3Ax.

Sistergroup homologue. In ground pattern of Dictyoptera, anal basivenale is subdivided by folds into a weak BAA1+2, well sclerotized but short BAA3+4, and a longer, bar-like BAP; jugal basivenale is articulated with the jugal arm of 3Ax (as in extant Blattodea; in Isoptera, BAA and BAP+BJ form long, broad plates and jugal arm (BJ) is absent; in Mantodea, jugal veins lost their basivenale and also their articulation with 3Ax by BJ) (Figs 11–13; Table 6F, G).

AP1+2

exc1 AP
rfc

af

AP4   tf

tf

JA

jugal cell

rc

ap3-ap4

anojugal cell

ring fold

AP4

rc

(A) "Labiduridae"

AP3

(B) Forficulidae

exc2

exc2

(C) Spongiphoridae

(D) Chelisochidae
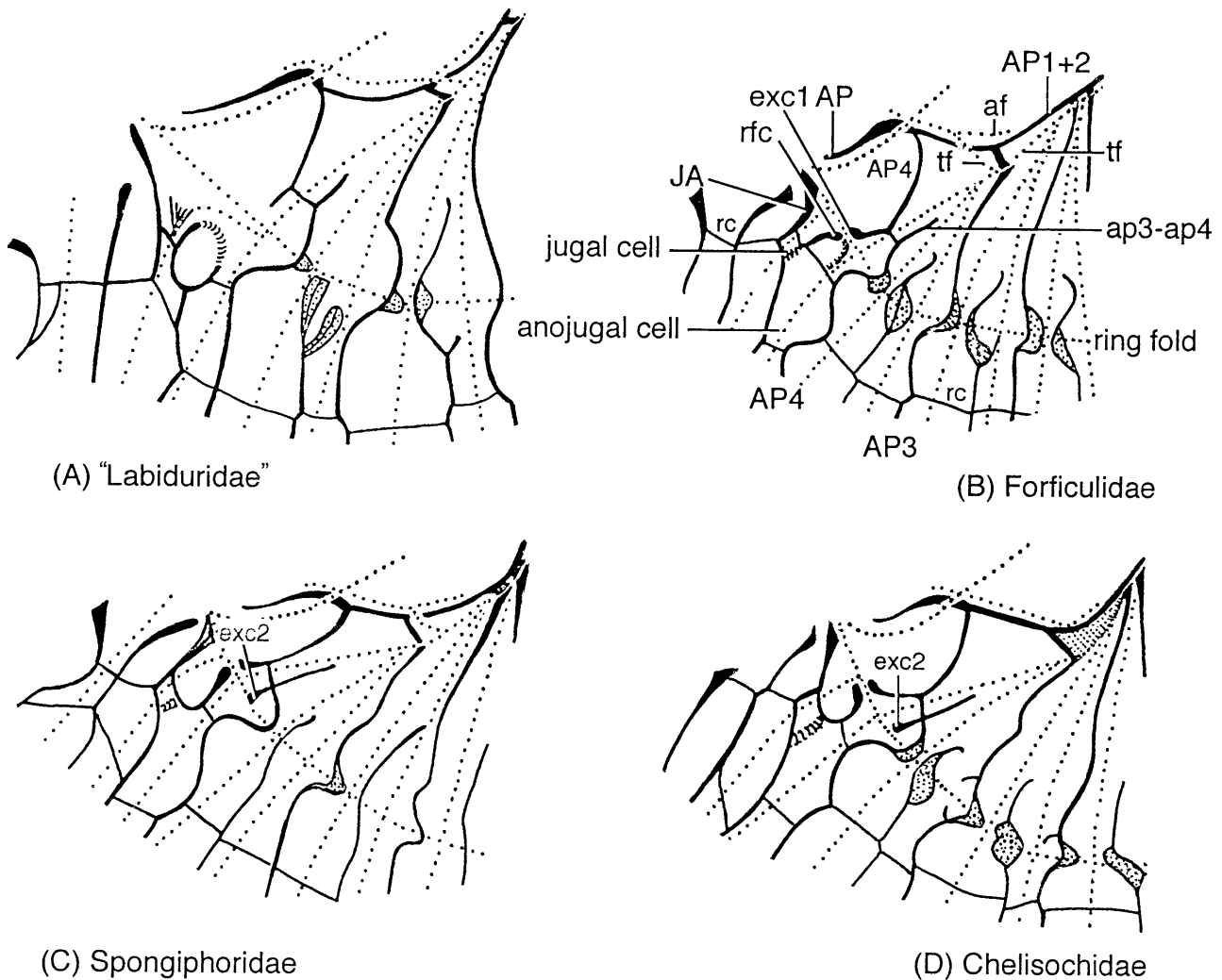
Fig. 6. Dermapteran anojugal lobe: The modifications in veinal support are characteristic for the different taxa.

Comments. In Hemineoptera + Endoneoptera, anal and jugal basivenalia are similar to those in Blattodea, but they are undergoing reduction (Figs 16, 17; Table 6B, D). Pleconeoptera + Orthoneoptera have a very different arrangement of folds and fields in the anojugal fan: All basivenalia (BAA1+2, BAA3+4, BAP, BJ) are robust and AA3+4 and AP are long (Figs 14, 15, 21; Table 6).

Anal brace (abr). In Dermaptera, the tip of BAA1+2 is articulated to medial basivenale (BM) and functions as highly unusual anal brace.

Sistergroup homologue. In Dictyoptera and all other Neoptera, the anal brace is between BAA1+2 and the distal end of Bcu.

Anal anterior (AA), anal posterior (AP). The anal anterior branches (AA) are strongly reduced. AA1+2 branches are lost. The arrangement of AA3+4 branches is unique. AA3+4 divides near base into AA3 and AA4. The short, strong and strut-like AA3 functions as a brace articulated, across the claval fold, with the equally strut-like base of CuP. The rest of AA3 is lost, or it flanks the claval fold as a weakly sclerotized strip. AA3 strip and CuP strip run along the claval fold (Figs 7–10). AA4, after a short distance, becomes fused with AP (Fig. 7A).

A suture separating AA4 and AP is actually the anal fold. The posterior anal sector (AP) is very strongly pectinately branched and provides the main support to the large anojugal lobe. AP basally diverges away from AA3+4, forms a loop spreading into a window and returns to fuse with AA4. The window is broad (Figs 7, 8A, C) or narrow (Figs 9, 10). The portion of AP distal from the window may be present (Figs 7, 8A), or membranized (Figs 8B, C, 9, 10). AP divides into AP1+2 and AP3+4 at about one third of the wing length (Fig. 5A).

AP1+2 base, after diverging from AP3+4, is obscured by the transverse fold (Figs 5A, B). AP1+2 sends out seven branches. The terminal branch has a long fork, so that the total number of so-called radiating branches is eight (the distal branch is numbered as 1st, and the most proximal branch as 8th). The branches of AP1+2 are crossed by transverse fold (Figs 2, 5, 6) separating its branches from AP1+2, either at a longer distance (Figs 5B, C, D) or at a shorter distance (Fig. 6).

AP3+4 almost immediately divides into a broad fork of AP3 and AP4. The base of AP3+4 is separated from the base of AP1+2 by the transverse fold in the continuation of the anal fold, causing a weakened spot in AP1+2. The

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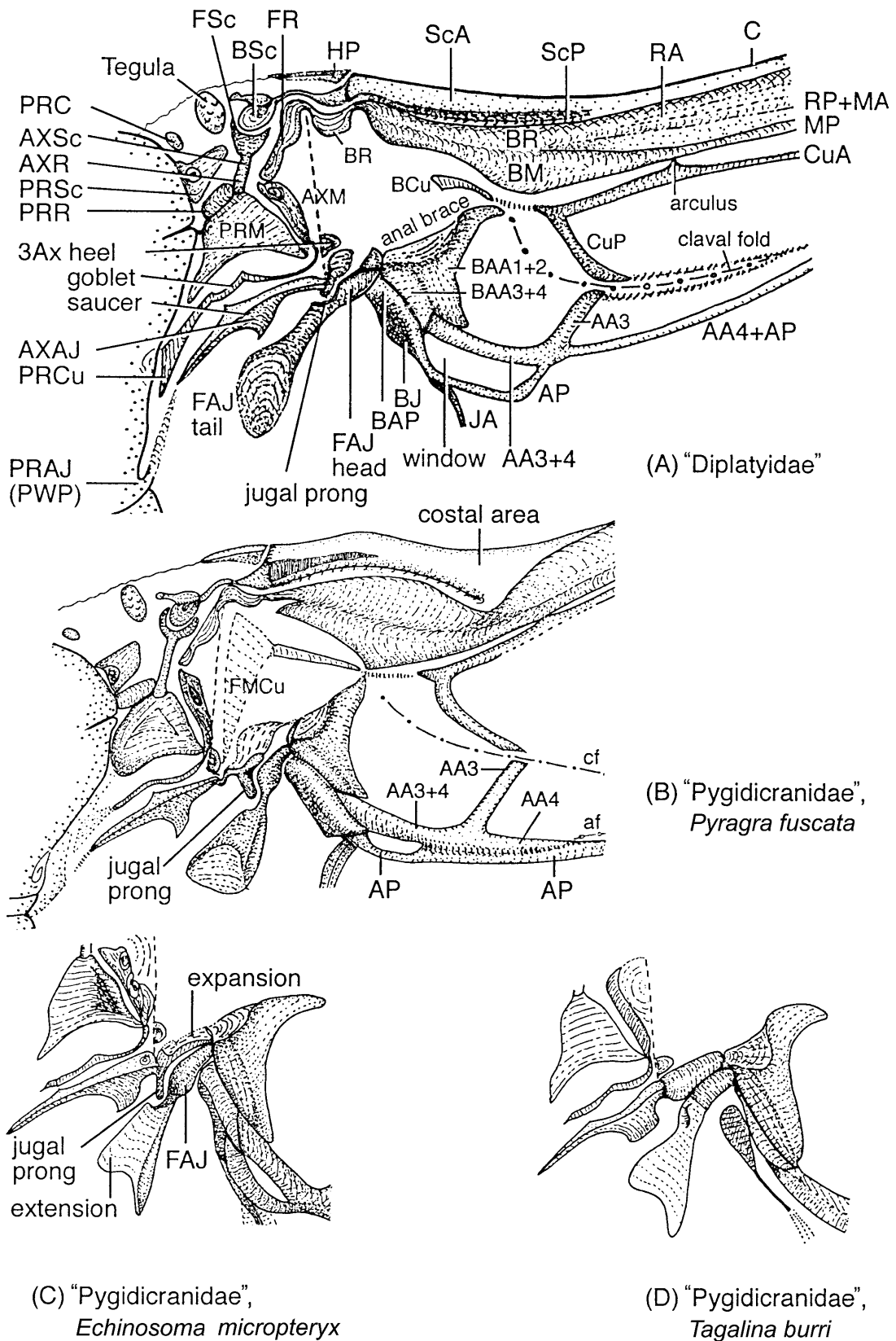
Fig. 7. Dermapteran hindwing base, fully homologized. For comparison with Dictyoptera, see Figs 11, 12, 13.

broad fork of AP3 and AP4 is present only in "Diplaty-idae" (Fig. 5A). In the other examined Dermaptera, the base of AP3 is superimposed on the weakened spot in AP1+2, so that the fork is absent. AP3 is located at an increasingly greater distance from AP4 and closer to the 8th radiating branch of AP1+2 (compare Figs 5B–E, 6).
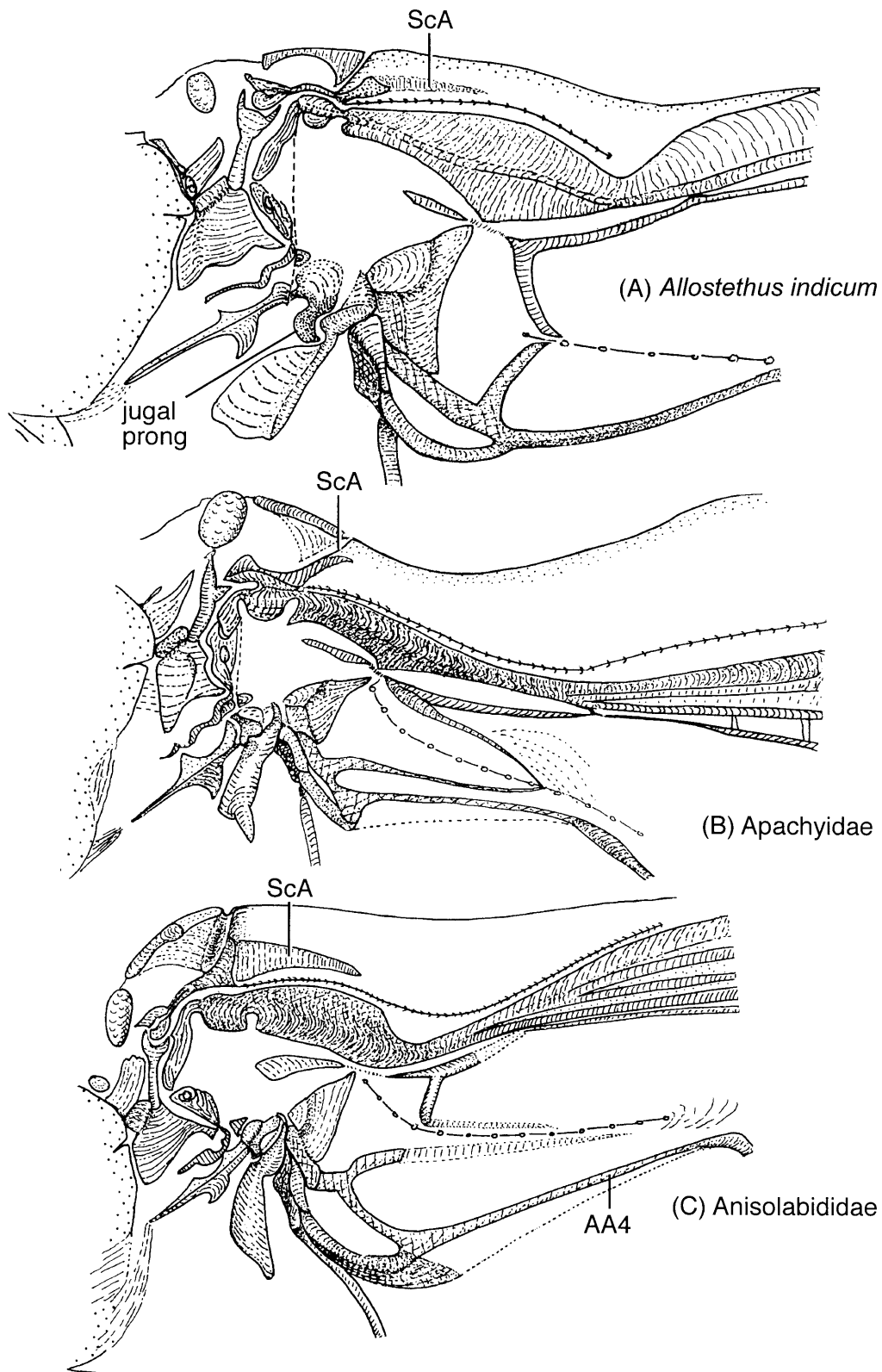
Fig. 8. Dermapteran hindwing base, fully homologized. For comparison with Dictyoptera, see Figs 11, 12, 13.

AP3 and AP4 are connected by a long, oblique cross-vein ap3-ap4, flanked by a radiating fold.

The bend in AP4 is either simple (Figs 5A–C), or it may be extended basally by an extension cross vein (**exc1**), so that the basal half of AP4 with the exc1 and

ap3-ap4 attached, resembles the **letter "H"** (Figs 5D, E, 6A, B). In Spongiphoridae and Chelisochidae, ap3-ap4 can be extended to the other side of AP4 (**exc2**), and in this case, AP4 resembles a **buttressed letter "H"** (Figs 6C, D). AP4 is strongly indented at the ring fold (Figs 5,
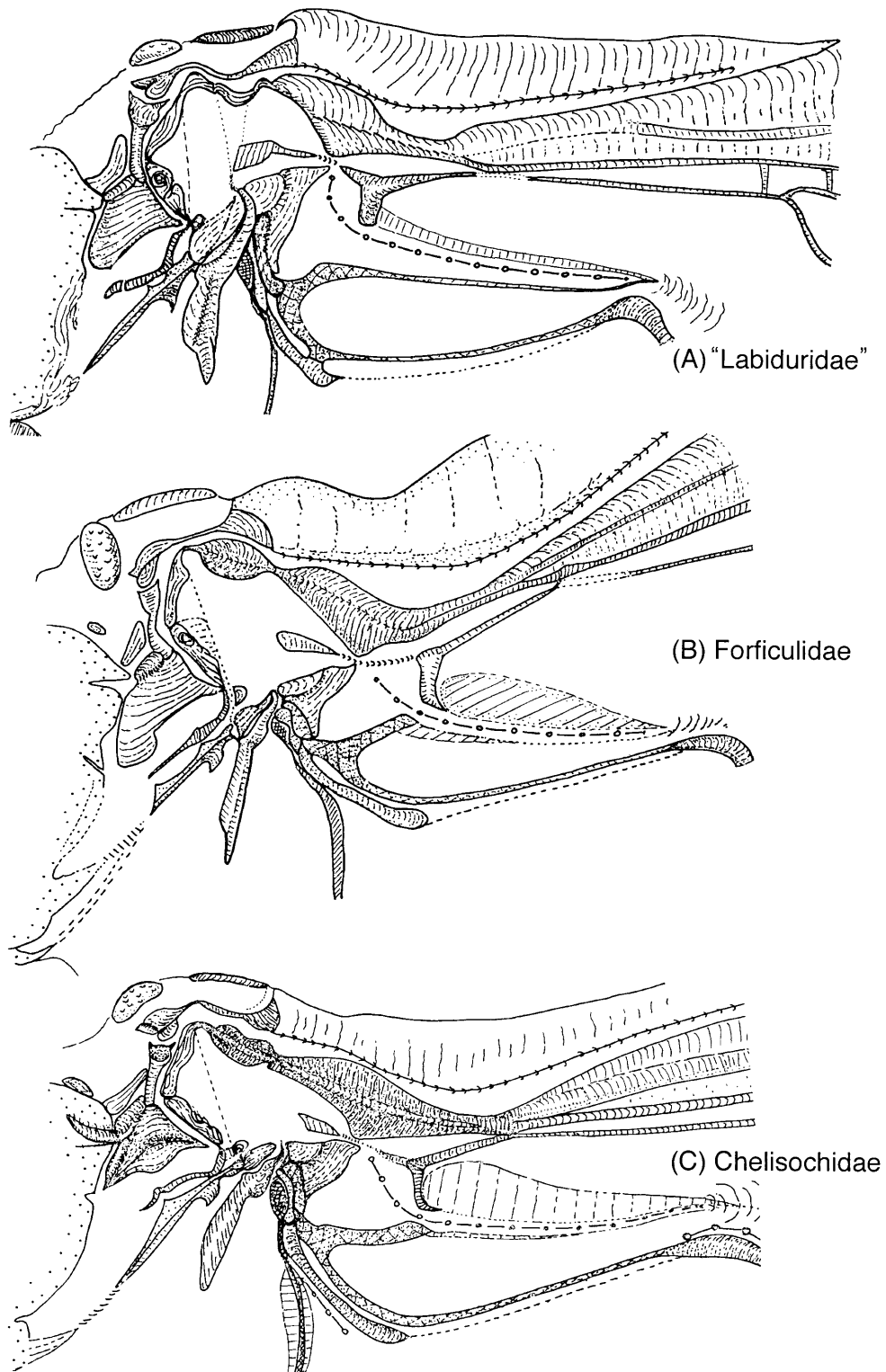
Fig. 9. Dermapteran hindwing base, fully homologized. For comparison with Dictyoptera, see Figs 11, 12, 13.

6A), then mildly curved before dissecting the ring cross-vein (**rc**). This curve is sinusoid and less pronounced in Spongiphoridae, Chelisochidae and Forficulidae (Figs 6B-D).

Stem line and sistergroup homologue. In *Apachelytron transversum*, the anals are quite similar to those of Dermaptera. The AA1+2 is absent, AA3+4 very short (not reaching the wing margin), AA3 forms a brace with CuP, and AA4 is simple and ends on the anal fold at about two thirds of the wing length (Fig. 3). AA4 and AP1+2 are separate and not fused. AP1+2 sends off 10 branches, the equivalent of dermapteran radiating

Spongiphoridae
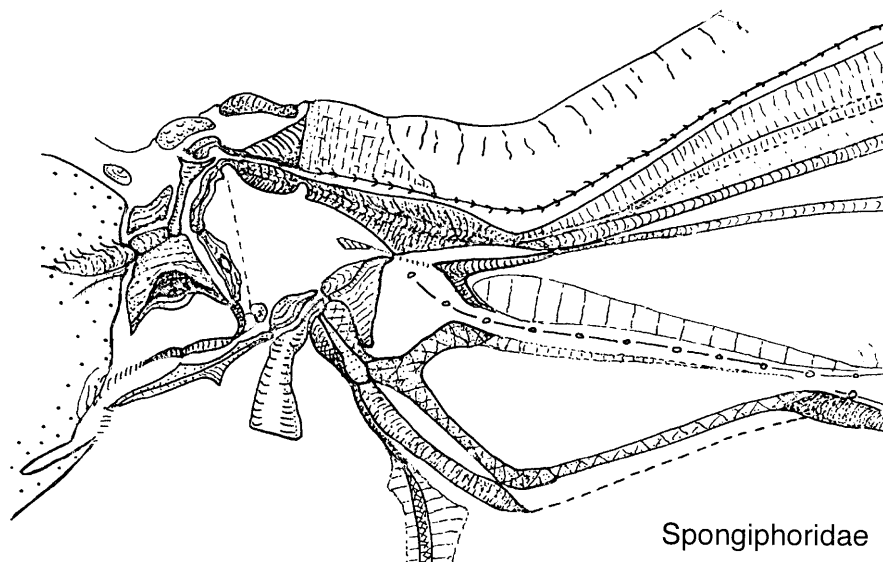
Fig. 10. Dermapteran hindwing base, fully homologized. For comparison with Dictyoptera, see Figs 11, 12, 13.

branches, and AP3+4 is twice forked. In ground pattern of Dictyoptera, the AA area is narrow and all AA branches are in a process of strong reduction (as in extant Blattodea + Isoptera, AA1+2 is weak, sometimes entering the claval fold, and AA3+4 bears few branches; in Mantodea, AA1+2 is absent and AA3+4 simple) (Figs 11–13; characters in Table 6D–G).

Comments. Note that in Blattoneoptera, Hemineoptera and Endoneoptera the AA area is combined with remigium in an extended **remigio-anal flight unit**, which ends at the anal fold. Therefore, their following **partial anojugal lobe unit** is supported only by the branches of AP and J (Figs 11, 12, 17, 21B, 22). In contrast, in Pleconeoptera + Orthoneoptera, the **remigial flight unit** ends at the claval fold. Therefore, their following **full anojugal lobe unit** is supported by the branches of AA, AP, JA, JP (Figs 1, 14, 15, 21A, 22).

Inner apical area. This narrow, triangular area lies between the outer apical area and the 1st radiating AP1+2 branch. It reinforces the anterior wing margin distally from the fustis (Fig. 2).

Stem line, sistergroup homologue and Comments. In *Apachelytron transversum* and in Dictyoptera, the homologous area, very small and inconspicuous is present (Fig. 3). There is no homologue in other Neoptera.

Jugal anterior (JA), jugal posterior (JP), ring fold cross-vein (rfc). The jugal sectors JA and JP are dichotomously branched in a unique way. JA divides into JA1+2 and a short JA3+4, which ends on JP1+2. The JA fork and the cross vein ja1+2-ja3+4 encloses the **jugal cell**, which is always crossed by the 10th radiating fold (Figs 5, 6). The jugal cell is an irregular triangle with an oblique base. Two cross veins are attached: A slightly curved ring fold cross-vein rfc and ap4-ja1+2 (Figs 5A, B, D). In Anisolabididae and "Labiduridae", the curvature of rfc has an arched fold in the membrane towards the middle of ap4-ja1+2, the end of which is sclerotized (Figs

5E, 6A). In the Eudermaptera (Spongiphoridae + Chelisochidae + Forficulidae), the triangle of the jugal cell is an open rectangle with one broad base (Figs 6B–D). The rfc is absent, replaced by a new arch composed of JA1+2 base, a part of ap4-ja1+2, and the sclerotized end of the **arched fold** (Figs 6C, D). In Forficulidae, the rfc is present but ap4-jp1+2 is shifted towards rfc, so that they meet (Fig. 6B).

A cell enclosed by AP4, JA1+2, ap4-ja1+2 and a ring cross-vein **rc** is called the **anojugal cell**. This cell is larger than the jugal cell and more or less rectangular (Figs 5A, B, E, 6A). In Forficulidae, Spongiphoridae and Chelisochidae, the anojugal cell is much larger than the jugal cell and irregular in shape (Figs 6B–D).

The dermapteran JP is absent and its two branches (JP1+2 and JP3+4) start in the membrane. JP1+2 is fused with the short JA3+4. Only the posterior part of JP3+4 is present in "Diplatyidae", "Pygidicranidae", *Allostethus indicum* and "Labiduridae" (Figs 5A–C, 6A) and it is absent in the other dermapteran taxa. The bent, posterior end of JA3+4 and the jugal cross vein form a zigzag pattern in "Diplatyidae" and *Allostethus indicum* (Figs 5A, C) or they are aligned (Figs 5B, E, 6B–D).

Stem line and sistergroup homologue. In *Apachelytron transversum*, jugal branches divide in a plesiomorphic way. JA divides into JA1+2 and JA3+4, and JP divides nto JP1+2 and JP3+4 (Fig. 3). In ground pattern of Dictyoptera, jugal branches JA and JP start from the jugal basivenale BJ and are repeatedly forked (as in stem-line blattoids and Isoptera; in Blattodea, JA branches are quite variable and tend to become pectinate to fill out space in an enlarged area; in Mantodea, jugal basivenale (BJ) is membranized) (Figs 11–13).

Comments. In Hemineoptera + Endoneoptera the jugal branches are undergoing strong reduction, probably as a synapomorphy. In Pleconeoptera + Orthoneoptera, plesiomorphic jugal branches JA and JP start from BJ, and are

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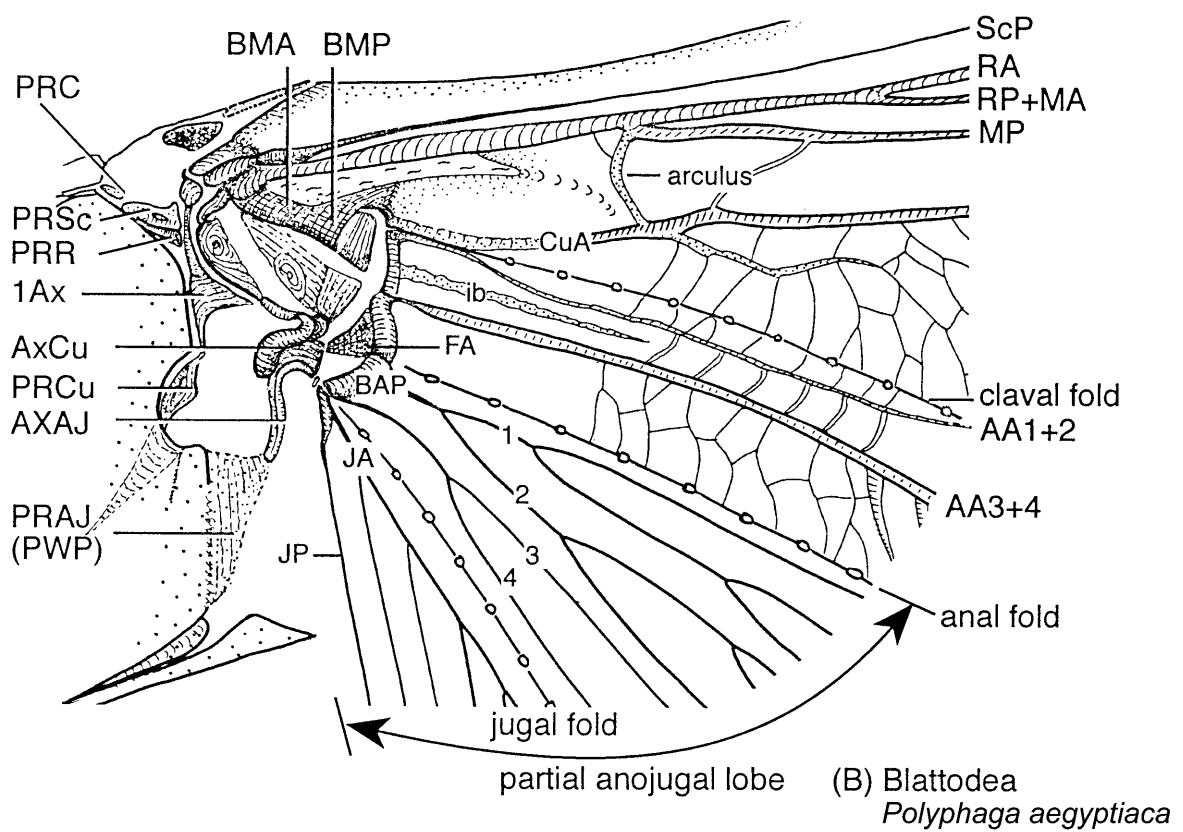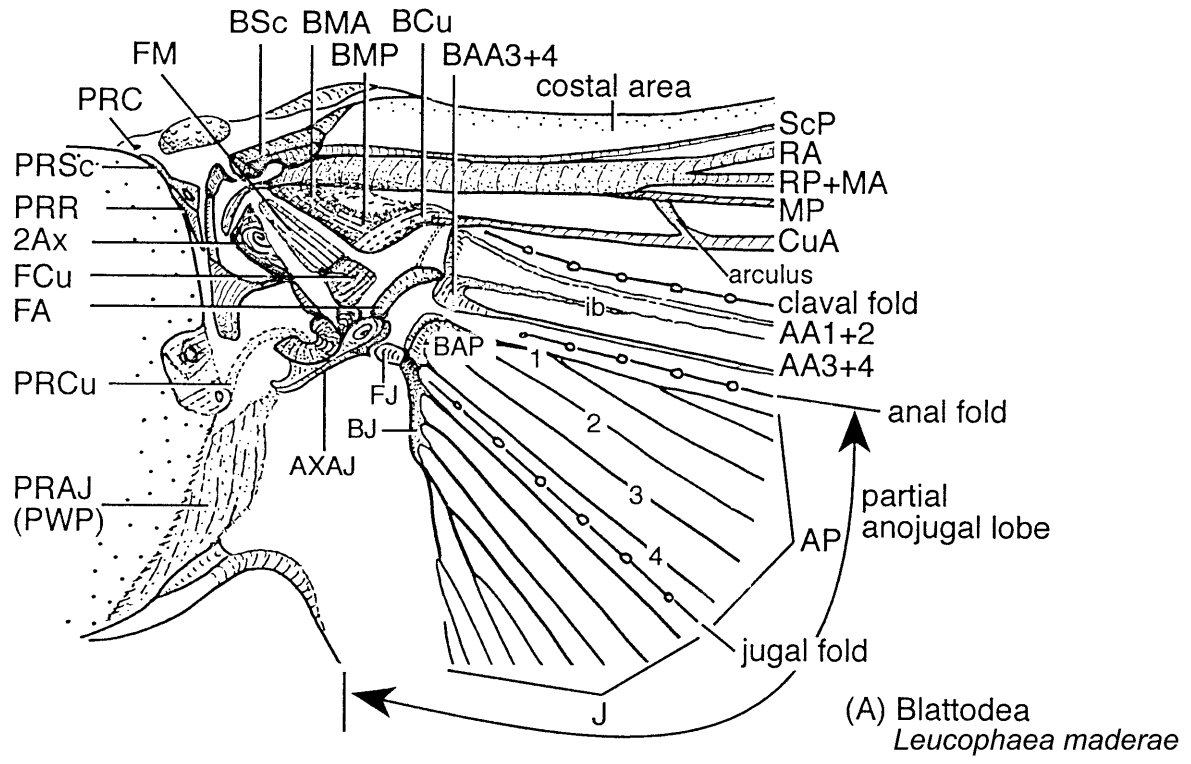
Fig. 11. Blattodean hindwing base. For comparison with Dermaptera, see Fig. 7A, Isoptera Fig. 12, and Mantodea Fig. 13. A – Blaberidae: *Leucophaea maderae*, hindwing; B – Polyphagidae: *Polyphaga aegyptiaca*, hindwing.

dichotomously branched (Figs 1, 14–17, 21; Kukalová-Peck, 1983) (Table 6B, C).

Anojugal lobe. In Dermaptera, the anojugal lobe is partial. It starts at the anal fold and is supported only by the
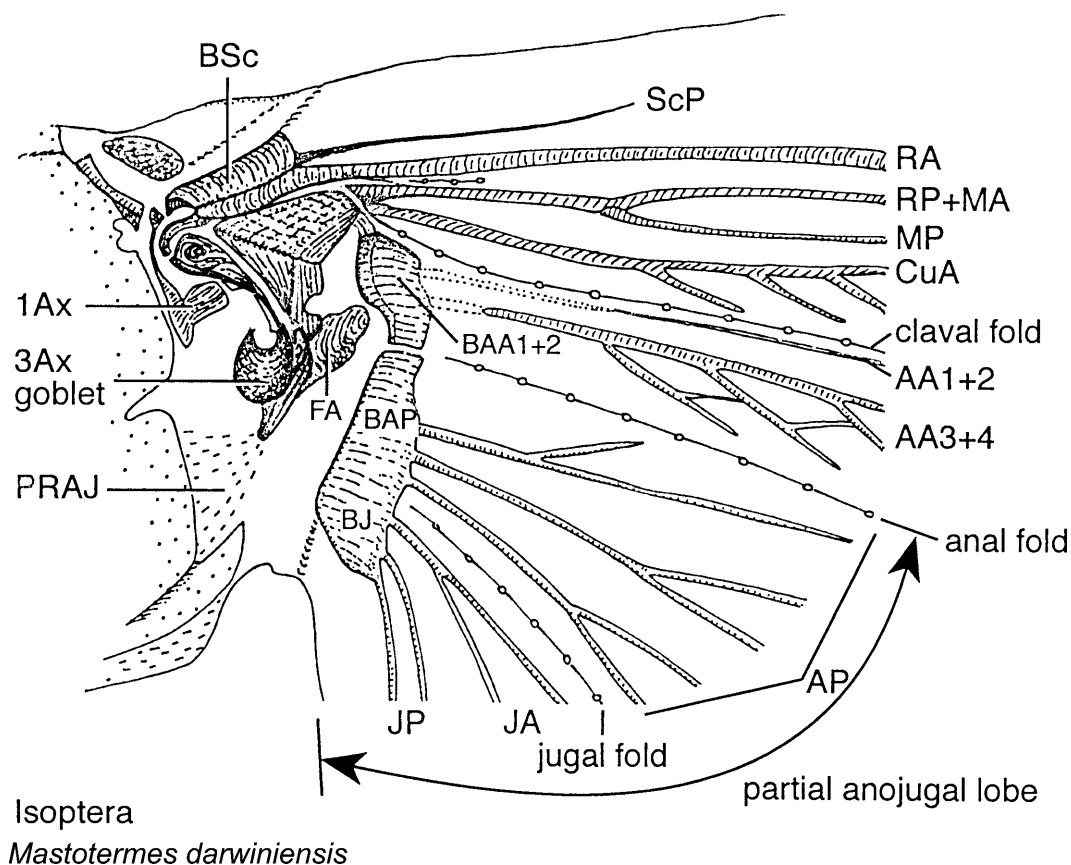
Fig. 12. Isopteran hindwing base. Isoptera: Mastotermitidae: *Mastotermes darwiniensis*, hindwing.

branches of the posterior anal sector AP, and of the jugal sectors JA and JP (Fig. 2). The lobe is very broadly attached to the metanotum, so that the wing attachment is actually much longer than the articulation. The functional importance of this phenomenon is discussed below.

Stem line and sistergroup homologue. The anojugal lobe in *Apachelytron transversum*, and in Dictyoptera, has the same composition as in Dermaptera (Figs 3, 11–13, 19–22.

Comments. The partial anojugal lobe in Hemineoptera + Endoneoptera has the same composition as in Blattoneoptera (Figs 3, 11–13, 16, 17, 22), but is usually much smaller. Broad, fully veined lobe occurs only in the basal representatives of Fulgoromorpha, Homoptera, Hymenoptera, Neuroptera, Megaloptera, Coleoptera, Strepsiptera, and Trichoptera. Pleconeoptera and Orthoneoptera have full anojugal lobe. It starts at the claval fold and is supported by all branches of the anal and jugal sector, AA1+2, AA3+4, AP1+2, AP3+4, JA1+2, JA3+4, JP1+2 and JP3+4 (Figs 14, 15, 22; Kukalová-Peck 1991, 1997; Kukalová-Peck & Brauckmann, 1992).

Ring cross veins (rc), ring brace (rbc). In Dermaptera, the unique chain of ring-shaped cross veins ends proximally with the rc between AP4 and JA. One or two rc cross veins may be added between JA1+2, JP1+2 and the attachment to the body (Figs 2, 5, 6).

The ring brace **(rbc)** is a chain of ring cross veins **(rc)** spanning between the AP1+2 anal, jugal and intercalary branches, which keeps them apart. It was formerly called "vena spuria" (Giles, 1963; Kleinow, 1966). The orientation of the rbc, placed between the posterior jugal branches and the end of JA3+4, varies. The rbc is zigzagged in "Diplatyidae" and *Allostethus indicum* (Figs 5A, C), but it is fully aligned in all other Dermaptera (Figs 5B, D, E, 6).

Folds and areas in Dermaptera hindwings

Claval fold (cf). The claval fold is shallow, empty, and very short, starting at the cubital basivenale and ending between the 8th radiating branch and AP3+4 (Figs 7–10).

Stem line and sistergroup homologue. In *Apachelytron transversum*, the claval fold is somewhat longer than in Dermaptera but it also ends far from the wing margin. CuP probably descended to its bottom (Fig. 3). In ground pattern of Dictyoptera, the claval fold is directed towards the posterior margin as in other Neoptera, but it is shallow, especially near the posterior margin, flanked distally by CuP, and claval furrow is probably devoid of veins. (In extant Mantodea CuP descends to the bottom line of claval furrow; in Blattodea, the furrow is either devoid of veins, or AA1+2 descends temporarily to its bottom line; in Isoptera, it is devoid of veins; in blattoid stem line it probably contained CuP (as in Carboniferous forewings), but this observation needs additional verification).

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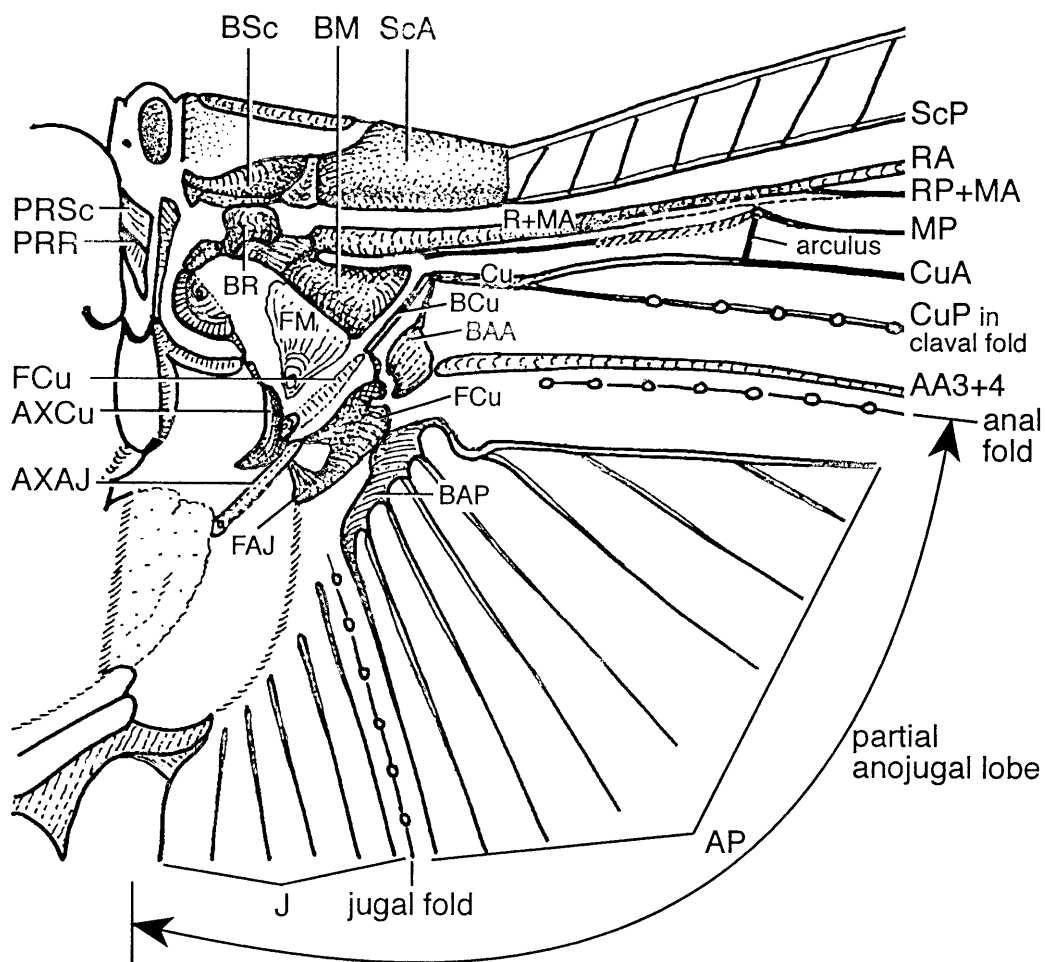
Mantodea
Polypsilota aeruginosa

Fig. 13. Mantodean hindwing base. For comparison with Dermaptera, Blattodea and Isoptera, see Figs 7–13. Mantidae: *Polypsilota aeruginosa*, hindwing.

Comments. In Hemineoptera + Endoneoptera the bottom line of claval fold is devoid of veins, shallow, and often shortened, as in Dictyoptera (Figs 1, 15, 17, 21A). In Endoneoptera the claval fold is flanked proximally by the anal branch (Fig. 15). In Orthoneoptera + Pleconeoptera, the claval fold is deeply incised and serves as the main flexion line during flight (Figs 14, 15).

Anal fold (af). The anal fold is difficult to distinguish from numerous other wing folds (Figs 5–10). The anal fold runs basally between AA3+4 and AP and crosses the membranous window, but its next section is obscured by a fusion between AA4 and AP and is expressed only as a suture. Anal fold reappears beyond the end of AA4 and runs for a short distance anteriorly close to AP and AP1+2, while becoming increasingly shallow until it disappears in the membrane.

Stem line and sistergroup homologue. In *Apachelytron transversum* (Fig. 3), and in Dictyoptera (Figs 11–13), the anal fold separates two distinctive flight units: The remigium combined with the largely reduced AA, and the anojugal lobe supported by the AP and J branches. The anal fold is the main fold along which the anojugal lobe folds at rest underneath the remigium. In the most primitive blattoid folding type, present in the Palaeozoic blattoid stemgroup and also in the extant Isoptera, the anojugal lobe folds flatly underneath the remigium as a book folds along a straight spine (Kukalová-Peck & Peck, 1993).

Comments. In Hemineoptera + Endoneoptera (Figs 16, 17) the most primitive hindwings in the early ancestral hemipteroids (Paoliidae), with relatively small anojugal lobe, are flexed backwards in an oblique, postero-lateral position without crossing each other (probably somewhat rooflike), and the anojugal lobes do not fold at all (Kukalová-Peck & Brauckmann, 1993). The "book-like" folding of the anojugal lobe, similar to that in the blattoid stem line and Isoptera, is found in modern Coleoptera and to a degree in Hymenoptera. Thus, the evolutionary steps seem to proceed from "incomplete flexing, no folding" to "complete flexing, book-like folding", which is then combined with irregular "fan-like folding" until the latter prevails. In contrast, in Pleconeoptera and Orthoneoptera, the
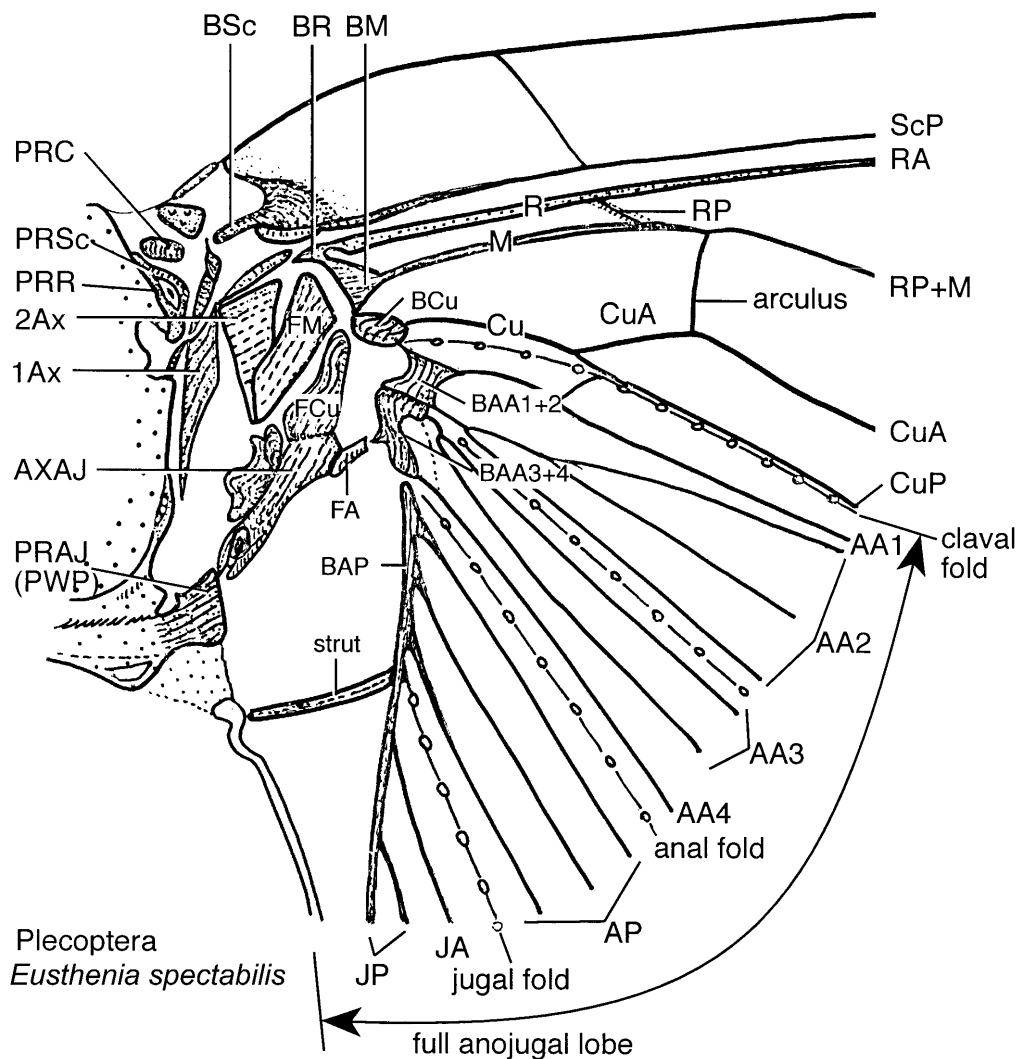
Fig. 14. Pleconeopteran hindwing base. Unlike in Dermaptera and Dictyoptera, full anojugal lobe is present. Plecoptera: Eustheniidae: *Eusthenia spectabilis*, hindwing.

anojugal lobe starts at the claval fold, the principal flexion line in flight (Brodsky, 1994) (Figs 14, 15, 21, 22). The anal fold is one of several much less important folds, and the lobe folds like a regular fan.

Following folds are autapomorphic for the Dermaptera and cannot be compared with the stem line, sistergroup or other taxa described here.

Ring fold (rf). This autapomorphic, semicircular fold starts at the wing articulation and ends at the anterior wing margin distally from the inner apical area (Figs 2, 5, 6). The ring fold crosses straight or arched indentations in AP1+2 branches (radiating branches) which are broadened and reinforced by sclerotized membrane. It is also supported by broadenings in the intercalary branches (ib, Fig. 2), which are arched in the opposite direction. These broadenings play a very important role in the automatic dermapteran wing folding (see below).

Radiating folds. These autapomorphic folds start from the bases of the radiating branches and end at the posterior wing margin (Figs 2, 5, 6). The area between two adjacent radiating folds represents one sector of the hindwing fan, containing a radiating branch (AP1+2

branch), or an intercalary branch (ib). Radiating folds are numbered according to the custom, starting with the most distal fold next to the inner apical area and counting in a proximal direction. The radiating folds alternate between convex and concave positions, starting with the convex fold proximal to the inner apical area.

Transverse fold (tf). This autapomorphic fold starts in "Diplatyidae" (Fig. 5A) proximally from the fork in AP into AP1+2 and AP3+4, and cuts off the base of the AP1+2 branch. In all other Dermaptera, the base of AP1+2 is obscured and tf crosses AP either distally (Figs 5B, C, E, 6A, C, D), or proximally (Fig. 6B) from the base of AP3. Then, tf curves towards the distal end of the fustis. It dissects on its way the bases of the radial branches either close to or somewhat distant from, their AP stem and reaches the anterior wing margin between the fustis and the outer apical area (Figs 2, 5, 6).

Longitudinal fold (lf). The autapomorphic fold lf starts in the wing articulation and runs as a convex fold posterior to the squama (and posterior to AP). It flanks anteriorly the ulnar area and crosses tf at the distal end of the fustis. Fold lf changes into a concave fold, continues run-

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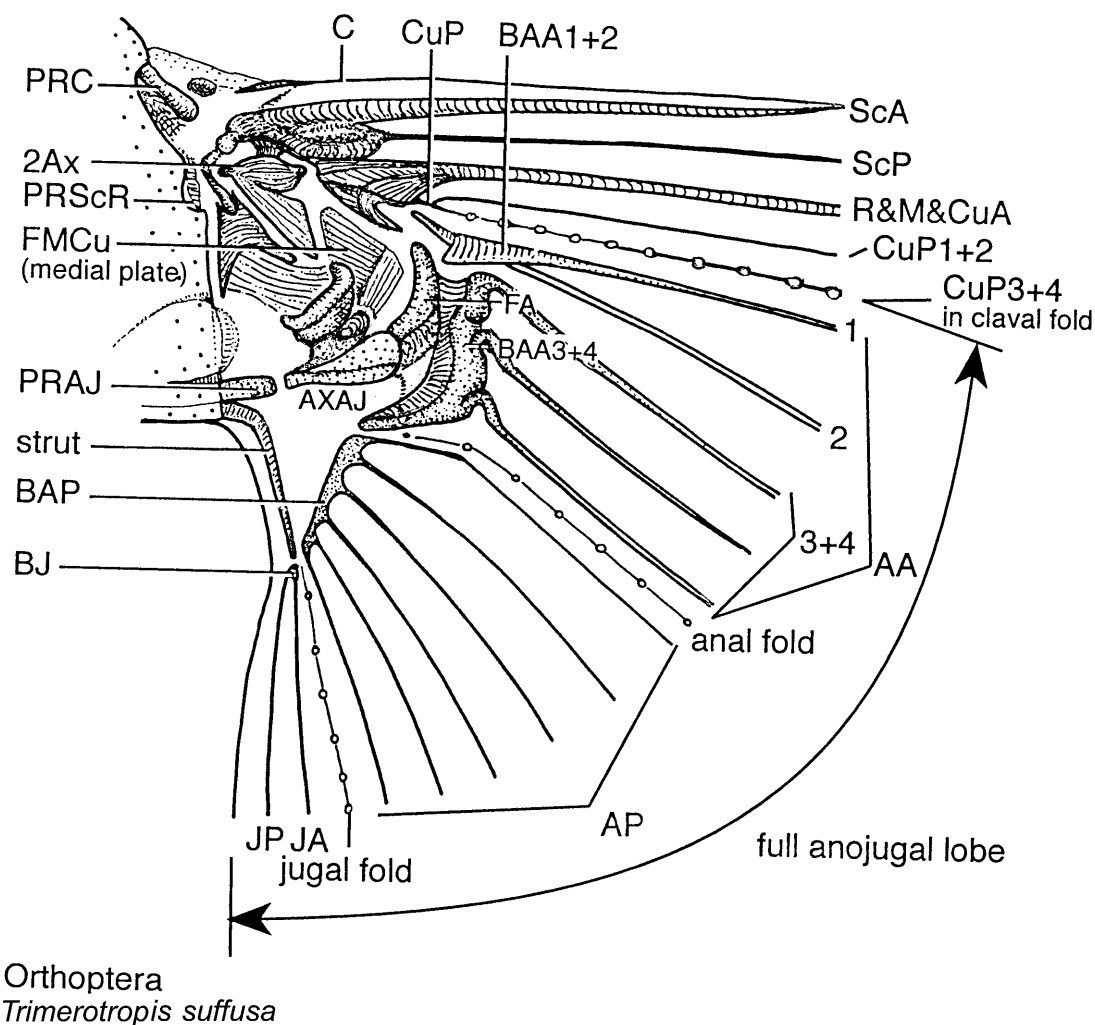
Fig. 15. Orthoneoptera, Caeliferan hindwing base. Unlike in Dermaptera and Dictyoptera, full anojugal lobe is present. Orthoptera: Caelifera: Acrididae: *Trimerotropis suffusa*, hindwing.

ning between the outer and inner apical area, and ends on the anterior apical wing margin (Fig. 2).

Squama. This autapomorphic area is delimited anteriorly by the anterior wing margin, distally by tf, posteriorly by lf, and proximally by the wing articulation. Squama forms the dorsal surface of the wing package at rest. The proximal part of the squama is covered by the tegmen and the uncovered distal part is the fustis head (Fig. 2).

Ulnar area. This autapomorphic area lies posterior to lf, proximal to tf, and anterior to rf. It is supported by AP1+2 and AP4, and ap3-ap4 is close to its posterior border. The ulnar area is the ventral surface of the wing package at rest. In the wing package the large anojugal fan lies folded between the squama and the ulnar area (Fig. 2).

Outer apical area. This autapomorphic area forms the anterior apical wing margin distal to the squama. It is delimited posteriorly by lf and proximally by tf (Fig. 2).

Inner apical area. This autapomorphic area is delimited anteriorly by lf, posteriorly by the anojugal fan, and proximally by the tf (Fig. 2).

Anojugal fan. This autapomorphic fan constitutes almost the entire wing except the squama, ulnar area, and outer and inner apical area (Fig. 2).

Hindwing articulation

The following is the description of the articular elements. The symbols for the precostal row of sclerites (PC) are left out for convenience, because in Dermaptera the PC and C sclerites are all fused without a suture. In contrast to the wing venation, the wing articulation is not visible in any neopteran fossils, including *Apachelytron transversum*.

Tergal fissures. The three neopteran tergal fissures, radio-medial, medio-cubital and cubito-anal (Fig. 1) are present in "Diplatyidae" (Fig. 7A) and occasionally in well sclerotized Forficulidae (Fig. 9B). Most of the dermapteran specimens have only the radio-medial fissure (for example, Fig. 9C).

Sistergroup homologue. In ground pattern of Dictyoptera, the medio-cubital fissure is obscured and the radio-median and cubito-anal fissures are weakly indicated (as in extant Mantodea and Isoptera; they are obscured in Blattodea).
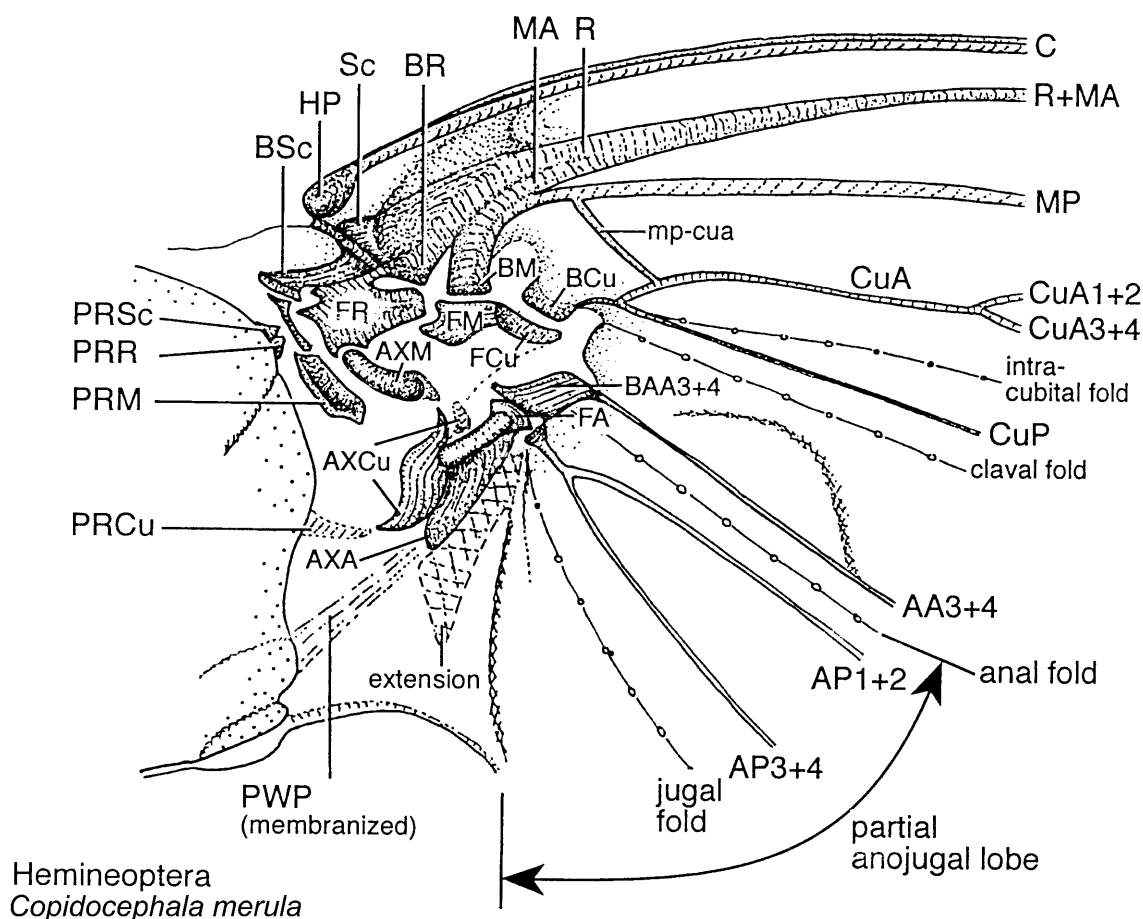
Fig. 16. Hemineopteran hindwing base. Partial anojugal lobe. Hemiptera: Fulgoromorpha: Copidocephalidae: *Copidocephala merula*, hindwing.

Comments. The fissures are variably retained and also obscured in Hemineoptera + Endoneoptera (Figs 16, 17) and in Pleconeoptera + Orthoneoptera (Figs 14, 15).

Proxalaria, precosto-costal proxalare (PRC). The PRC is a small sclerite near the tergum. PRC is aligned with the tegula, the humeral plate (HP), and the costal wing margin (all these elements in Neoptera are composed of the precostal and costal row fused together).

Sistergroup homologue. In Dictyoptera, and all other Neoptera, PRC is similar as in Dermaptera (Figs 7–11).

Comments. PRC in Neoptera hindwings is unconnected, variously reduced and insignificant. But, the homologue of PRC is important in Palaeoptera (Kukalová-Peck, 1997, Fig. 19.7a, b; 19.8a, b) (Table 6A).

Subcostal proxalare (PRSc), radial proxalare (PRR), anterior wing process (PRScR). In Dermaptera, the two proxalaria are widely separated one from another (rather than fused) and articulated with the tergum by membrane (Fig. 7B). PRR is unique in being firmly hinged or fused with 1Ax tail (PRM) (Figs 8–10).

Sistergroup homologue. In Dictyoptera, PRSc and PRR are also primitively articulated with the tergum, but they are fused together and separated only by a suture (Figs 11–13).

Comments. In ground pattern of Hemineoptera + Endoneoptera, subcostal and radial proxalare are also separated and articulated with the tergum by a membrane (as in extant Endoneoptera, Fig. 17; in extant Hemineoptera these sclerites are variously reduced, Fig 16). In Pleconeoptera, PRSc and PRR are secondarily fused with the tergum forming the anterior wing process. In Orthoneoptera, the anterior wing process is reduced. Note that the subcostal and radial proxalare were both traditionally, but erroneously, interpreted as a "tergal outgrowth". Instead, they originate from the same anlage as the other articular sclerites and the wing itself (Stenzhorn, 1974; Kukalová-Peck, 1983, 1997).

Medial proxalare (PRM). In Dermaptera, this sclerite forms a very large tail of 1Ax. It articulates proximally with the tergum and distally with 2Ax body (AXM). Anteriorly it is uniquely firmly hinged with PRR. 1Ax tail (PRM) is separated by a suture from the fully fused 1Ax waist + neck + head. The posterior margin varies from concave (Fig. 7A) to lobate (Figs 7B–D) and wavy (Figs 9C, 10).

Sistergroup homologue. In ground pattern of Dictyoptera the 1Ax tail is much less massive (in extant Blattodea + Isoptera; in Mantodea, the tail is very narrow, with a large posterior embayment) (Figs 11–13).

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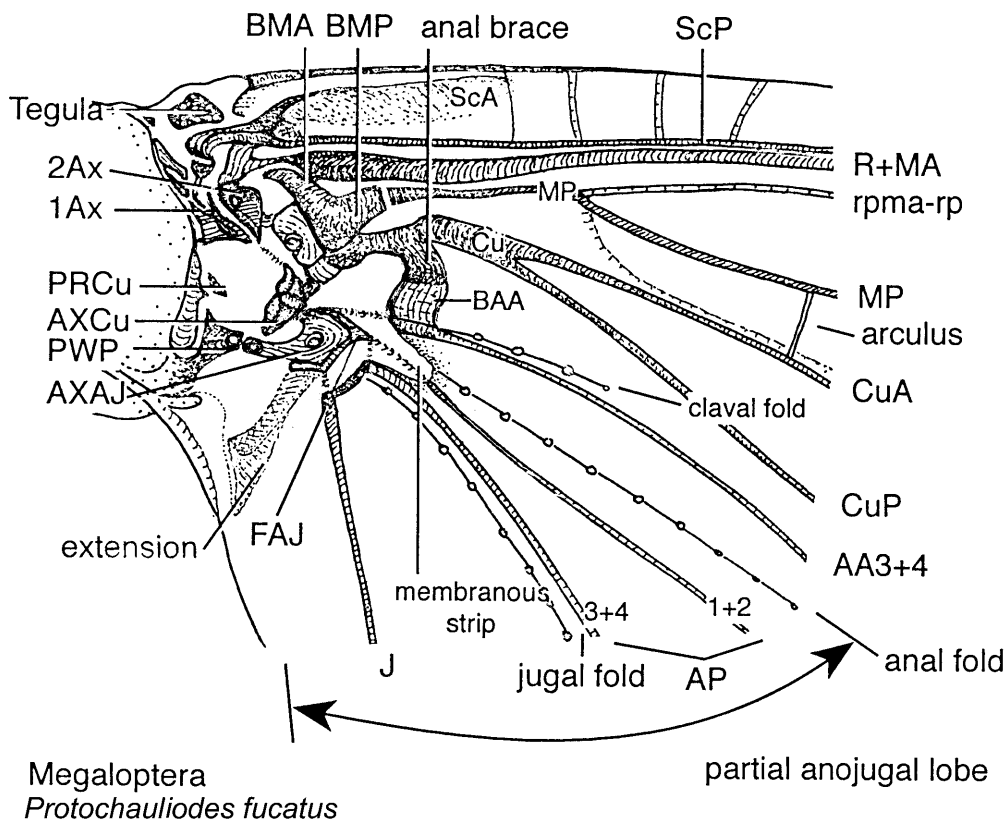
Fig. 17. Endoneopteran hindwing base. Partial anojugal lobe. Megaloptera: Corydalidae: *Protochauliodes fuscatus*, hindwings.

Comments. The 1Ax tail in Hemineoptera + Endoneoptera and in Pleconeoptera + Orthoneoptera is mostly less massive than in Dermaptera and quite variable. No informative higher-level character states were found (Figs 14–17).

Cubital proxalare (PRCu). The dermapteran PRCu is present in "Diplatyidae" (Fig. 7A) as a long, narrow sclerite articulated to the tergum and to the 3Ax goblet (AXCu). In the rest of Dermaptera, PRCu is partly (Figs 7B–D, 8B, C, 9, 10) or fully (Fig. 8A) membranised, starting at its proximal end, so that 3Ax goblet sometimes has a small remnant of PRCu attached to it (Fig. 9C).

Sistergroup homologue. In ground pattern of Dictyoptera, PRCu is membranised, only a strip of stiff membrane remains (as in some extant Blattodea only, Fig. 11A; PRCu is completely membranized in Isoptera and Mantodea) (Figs 12, 13).

Comments. In Neoptera, PRCu is reduced or lost. It occupies the same "window" into which 3Ax collapses when wings are flexed over the abdomen. Besides Dictyoptera, ribbon-like, pliable PRCu is preserved in Hemineoptera, in Psocoptera (JKP, personal observation) and Fulgoromorpha (Fig. 16). Disjunct fragments occur in Endoneoptera in Megaloptera (Fig. 17) and Neuroptera (Ithonidae, Rapismatidae, Dilaridae) (JKP, unpublished observation). In Pleconeoptera and Orthoneoptera, PRCu is completely lost (Figs 14, 15). The PRCu is well developed in Palaeoptera (Kukalová-Peck, 1983, 1997).

Anal proxalare (PRA), jugal proxalare (PRJ), posterior wing process (PWP or PRAJ). In Dermaptera, the posterior wing process (PWP) is membranized.

Sistergroup homologue. In Dictyoptera, the posterior wing process is also membranised (Figs 11–13). This is an important synapomorphy shared by all Blattoneoptera.

Comments. Membranized PWP, if found in Zoraptera, would be very informative about their relationship. Note that PWP is actually the fourth axillary (4Ax), which became secondarily fused with the tergum. In Endoneoptera 4Ax is very rarely preserved, in Hymenoptera (JKP, unpublished observation) and in Coleoptera: Gyrinidae (Kukalová-Peck & Lawrence, 1993). A well sclerotized PWP was formed many times at many taxonomic levels. In Hemineoptera PWP is highly variable (e.g., it is membranized in some Fulgoromorpha, Fig. 16). In Orthoneoptera 4Ax is sometimes present; in Pleconeoptera PWP is firmly hinged or fused with the tergum (Figs 14, 15).

Precosto-costal axalare (AXC), tegula. In all neopterous wings, including those of Dermaptera and Dictyoptera, AXC is incorporated into the tegula, a sensory organ.

Humeral plate (HP, FPCC + BPCC). The sclerites in the composite sclerite HP are smoothly fused, HP is long and very narrow and it is extended posteriorly by a triangle of stiff membrane (Figs 7, 8, 9A).

Sistergroup homologue. In Dictyoptera, the humeral plate is similar to that in Dermaptera, also smoothly fused, but without the posteriorly stiffened membrane (Figs 11–13).
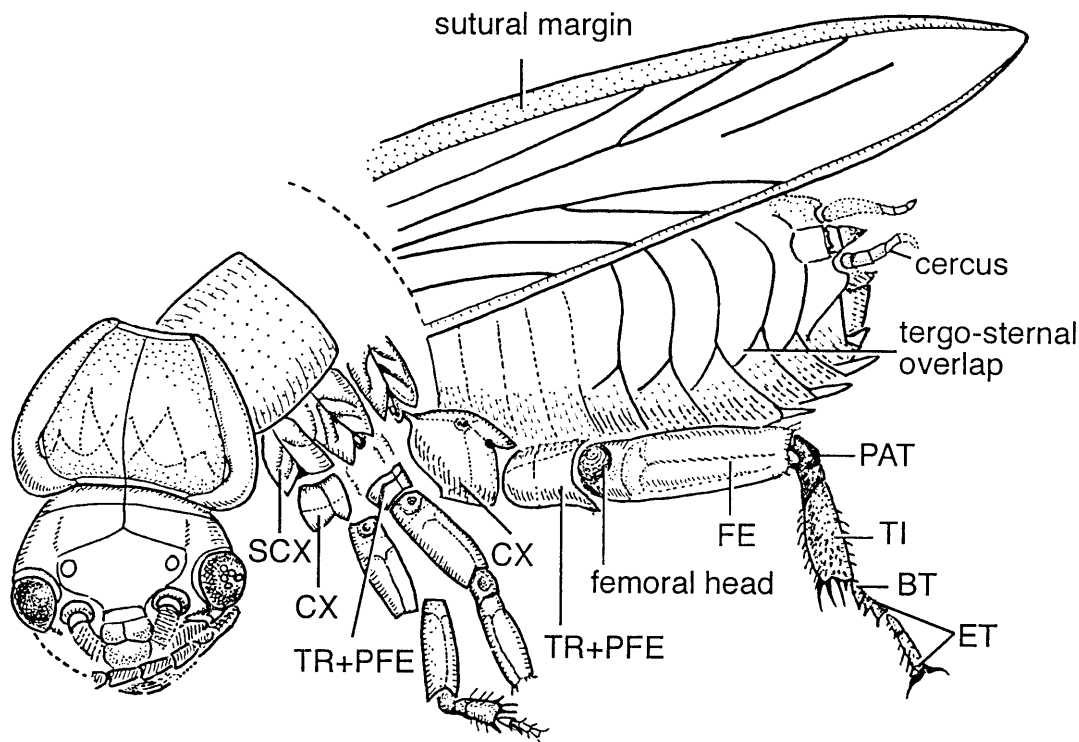
Fig. 18. Representative of dermapteran stem line Permelytridae, *Acosmelytron delicatum*, Lower Permian of Kansas, USA. Based on holotype no. 5416, Peabody Museum, Yale University, New Haven, USA. Left elytron length about 6 mm.

Comments. The neopteran HP is composed of four fused sclerites, the precosto-costal basivenalia and the precosto-costal fulcalaria (Fig. 1). Humeral plate sometimes shows the boundaries between the original four sclerites (e.g., in the Coleoptera: Browne and Scholtz, 1996). HP is unique for the Neoptera, but other than this, not very informative for the higher-level relationships.

First axillary (1Ax). The 1Ax head (FSc) is broad, very large, and bearing two long projections, which are extended to articulate with the lobate part of subcostal basivenale BScP (Fig. 7). The 1Ax neck (AXSc) and waist (AXR) are slender. The head, neck and waist are smoothly fused together, but they are still separated by a suture from the broad 1Ax tail (PRM, described above). The important, unique feature is the firm hinge between 1Ax tail and PRR.

Sistergroup homologue. In Dictyoptera, 1Ax head is smaller than in Dermaptera, and is separated by a suture from a relatively longer and thinner neck and waist, and a much smaller tail (Figs 11–13).

Comments. The 1Ax is an irregular, obliquely constructed neopterous axillary cluster composed of sclerites belonging to three rows (Sc, R, M) and three columns (PR, AX, F). The sclerites in 1Ax are primitively separated by sutures (best retained in Neuroptera forewings, in Ithonidae and Dilaridae, unpublished observation by JKP). 1Ax always articulates with the subcostal basivenale (Fig. 1). We did not find any characters that would reliably distinguish orders according to the morphology of 1Ax.

Second axillary (2Ax). In Dermaptera, the 2Ax body (AXM) is reduced to a thickened proximal margin, arched and twisted. The 2Ax arm (FR) is long, relatively thin and flexible with a small lobe in the middle (Figs 7, 8C) or near the distal end (Fig. 9B).

Sistergroup homologue. In Dictyoptera, 2Ax body (AXM) is also curved, weakened distally, wrinkled around muscular insertions and shaped like a human ear. The 2Ax arm (FR) is also weakly sclerotized and flexible, but thinner and shorter than in Dermaptera and the lobe in the middle is absent (Figs 11–13).

Comments. In Endoneoptera + Hemineoptera, the 2Ax body is also sigmoidally curved with a distinctly thickened proximal margin as an important synapomorphy. The 2Ax arm broadens anteriorly into a prominent lobe. In contrast, 2Ax in Pleconeoptera + Orthoneoptera is quite different. In Pleconeoptera (Figs 14) 2Ax bears a large, triangular, well sclerotized body (AXM), and 2Ax arm (FR) is articulated, short, slender, well sclerotized, movable and resting on the triangle like a lid. The large, sclerotized triangle and lid also occurs in Orthoneoptera (but in Caelifera the arm is relatively broad and is partially fused with the body, Fig. 15). The typically neopterous 2Ax is an irregular, obliquely constructed axillary cluster composed of two sclerites belonging to two different rows (R, M) and two columns (AX, F). The 2Ax body (AXM) always articulates proximally with 1Ax tail. 2Ax arm (FR) always articulates distally with radial basivenale (BR). The plesiomorphic condition is almost certainly a triangular body and a short, movable, articulated arm without any lobes. The 2Ax cluster offers several informative characters for higher phylogenetics (Table 6).
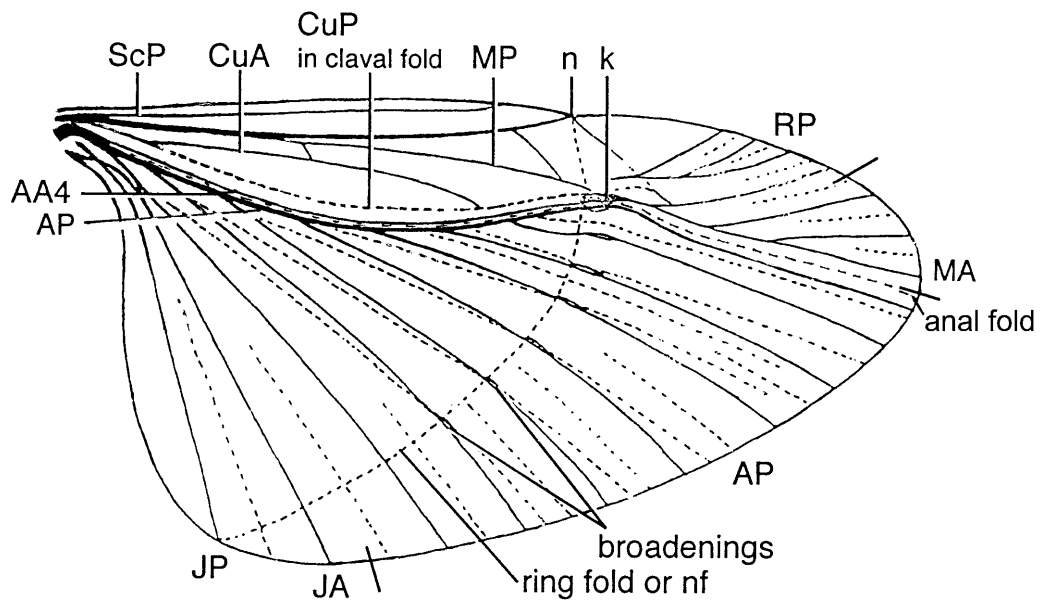
Fig. 19. The unfolded hindwing of *Protelytron permianum,* dermapteran stem line, Lower Permian, Kansas, USA. According to Tillyard's description, the fan is folded transversely along the ring fold and the veins have broadenings where they intersect the ring fold. The same is true in Dermaptera and we consider this to be a synapomorphy. After Tillyard (1931), veinal symbols according to Fig. 1.

Medial plate (FM and FCu, separate or fused). The medial plate is almost completely membranized. Well sclerotized Dermaptera (Fig. 7A) show a faintly pigmented remnant of the medial and cubital fulcalare (FMCu) fused into a single medial plate (Figs 7B–D).

Sistergroup homologue. In ground pattern of Dictyoptera, the medial plate is composed of two separate sclerites that are less membranized (in Mantodea only; in Blattodea + Isoptera, FM and FCu are fused; Figs 11–13).

Comments. In Hemineoptera + Endoneoptera (Figs 16, 17), FM and FCu are relatively well sclerotized, adjacent and separated by a suture. In Orthoneoptera, medial plate is very similar, only larger (Fig. 15). In Pleconeoptera, FM and FCu are separate and well sclerotized, and FCu is very broadly hinged with 3Ax saucer (Fig. 14). We found that the medial plate is quite variable and usually does not provide reliable higher-level characters, but there are a few exceptions, e.g., in Plecoptera (Fig. 14), and in Coleoptera (Kukalová-Peck & Lawrence, 1993).

Third axillary (3Ax). In Dermaptera, the 3Ax cluster is unique in many aspects. The 3Ax goblet (AXCu) is extremely long and thin and completely detached from the 3Ax saucer (AXAJ). 3Ax heel (AXCu, distal lobe) is separated from the goblet by a deeply incised fold, which also traverses the saucer. The saucer bears, near the middle, an anterior and posterior projection. The distal end of the saucer is traversed by a deeply incised fold and then expanded to provide a long articulation site, posteriorly for the large anojugal arm (FAJ), and anteriorly for the stiff membranous **expansion** (Fig. 7C). The arms of 3Ax are transformed as follows: The cubital arm (FCu) is part of the medial plate and desclerotized. The anal and jugal arm (FA and FJ) are fused into an anojugal arm, the **FAJ head**. This extends into the **FAJ tail**, a long, postero-

proximal extension formed by sclerotized membrane (Figs 7–10).

In "Diplatyidae", "Pygidicranidae" and *Allostethus indicum* the cap-like articulation of the saucer with FAJ is arched and bears a narrow **jugal prong,** which fits into a concavity on FAJ head (Figs 7, 8A). In the remaining Dermaptera the jugal prong is absent (Figs 8B, C, 9, 10). The conspicuous dermapteran anojugal arm (FAJ) bears an almost oval head and a tail. The head shows a faint suture between FA and FJ in "Diplatyidae", "Pygidicranidae" and *Allostethus indicum* (Figs 7, 8A). The tip of the head bears an anteriorly bent head projection articulated with the large triangular basivenale BAA1+2. The head is either enlarged, with a long narrow tip (Figs 8B, 9A), or short with a narrow tip (Fig. 8C), or its articulation with the 3Ax saucer is undulated (Figs 9B, C, 10). The tail of FAJ is a broad, weakly sclerotized extension in "Diplatyidae", "Pygidicranidae" and *Allostethus indicum* (Figs 7, 8A). In all other examined Dermaptera, it is strongly sclerotized, compact and much narrower (Figs 8B, C, 9, 10). The posterior margin of the head articulates with three fused basivenalia, BAA3+4, BAP and BJ.

Sistergroup homologue. In ground pattern of Dictyoptera, the 3Ax goblet, heel and saucer are close to the Neoptera reference scheme, but the anal arm FA is long and massive and the jugal arm very short (jugal arm is present only in Blattodea; in Mantodea the anal arm is widened and articulating not only with the usual BAA3+4, but also with BAP) (Figs 11–13).

Comments. In Hemineoptera + Endoneoptera (Figs 16, 17), the anal arm is fused with 3Ax saucer, as a synapomorphy, and the jugal arm is lost. In Pleconeoptera and Orthoneoptera, 3Ax is close to the Neoptera reference scheme, and the jugal arm is lost. The typically neo-

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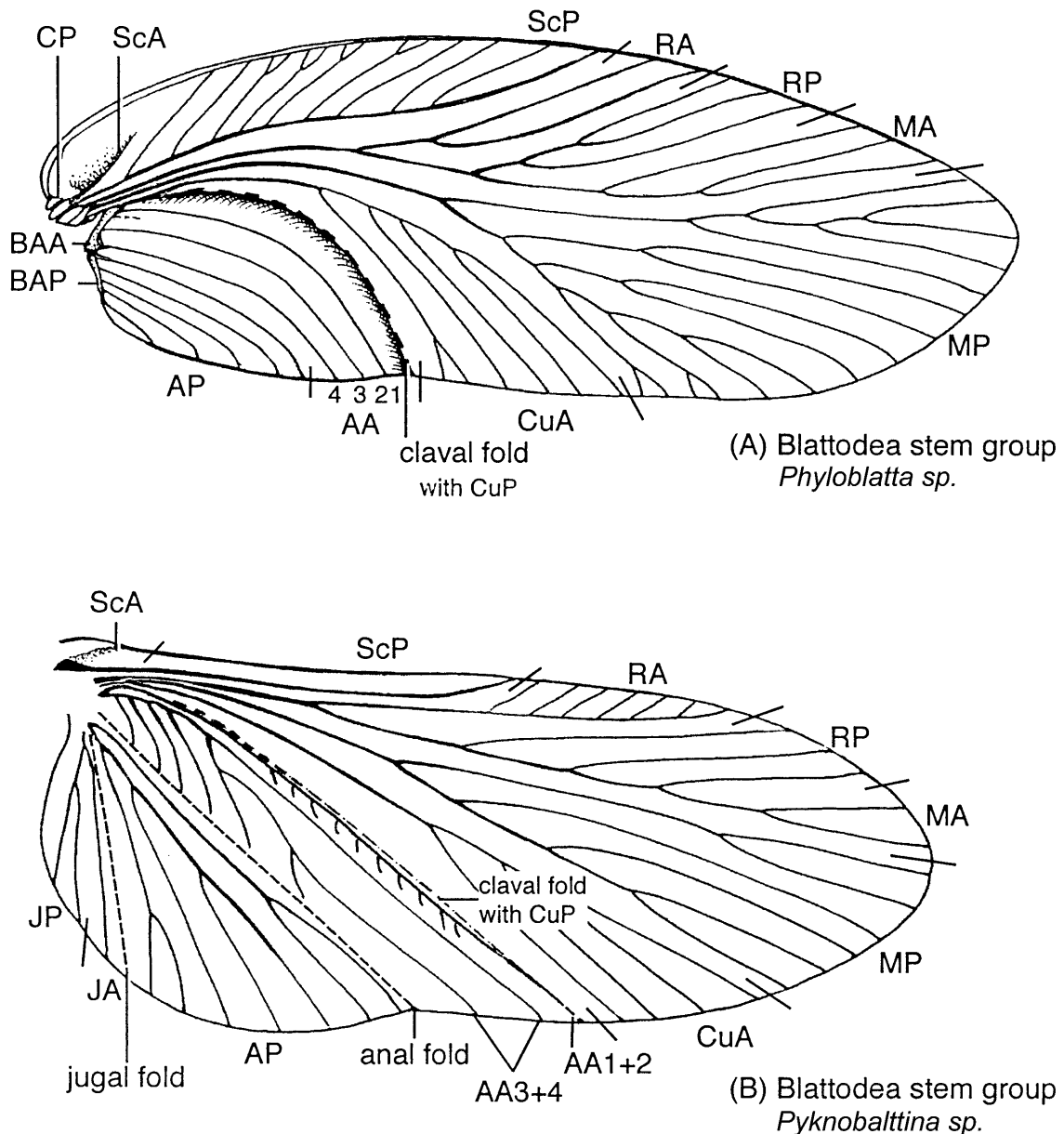
Fig. 20. Palaeozoic Dictyoptera, stem line: The ancestral anojugal lobe. A – in the forewing, bar-like BAA locks wings when flexed; reduced jugal lobe is tucked under the tegminous anal lobe; B – in the hindwing, veinal arrangement is radial, AA area is combined with the remigium; partial anojugal lobe starts at the anal fold. Archimylacridae, Lower Permian, Kansas, USA. After Kukalová-Peck, 1991, new interpretation.

pterous cluster 3Ax contains several phylogenetically informative higher-level characters. The axillary is composed of six sclerites belonging to three rows (Cu, A, J) and two columns (AX, F). In contrast with the obliquely constructed 1Ax and 2Ax, its sclerites are arranged in regular columns. The 3Ax contains a rotating body, and three arms. The 3Ax body is composed of three axalaria: AXCu, AXA, and AXJ. AXCu is subdivided by a deep, oblique fold into the proximal, large, protruding goblet, and the distal, small, sunken heel. AXA and AXJ are fused into AXAJ to form a saucer. The goblet and the heel articulate with the saucer. The proximal end of the goblet (AXCu) articulates with PRCu (Fig. 7A; note that PRCu in most Neoptera is membranized). The distal end

of the goblet articulates with the posterior tip of 2Ax body (AXM). The 3Ax manipulates three arms formed by three fulcalaria: FCu, FA and FJ. The 3Ax heel articulates with the **cubital arm** FCu. The saucer (AXAJ) articulates proximally with PRA and PRJ combined, primitively expressed as 4Ax, but usually fused with the tergum as the posterior wing process (PWP). The saucer articulates distally with the **anal arm** (FA), and the **jugal arm** (FJ). In Neoptera ground pattern, anal lobe is significantly enlarged and anal basivenale is divided into BAA1+2, BAA3+4 and BAP articulated one with another. The 3Ax anal arm (FA) always articulates with BAA3+4. The BAA1+2 serves in Neoptera as the anal brace with BCu. The three arms of 3Ax articulate distally with three veinal

473
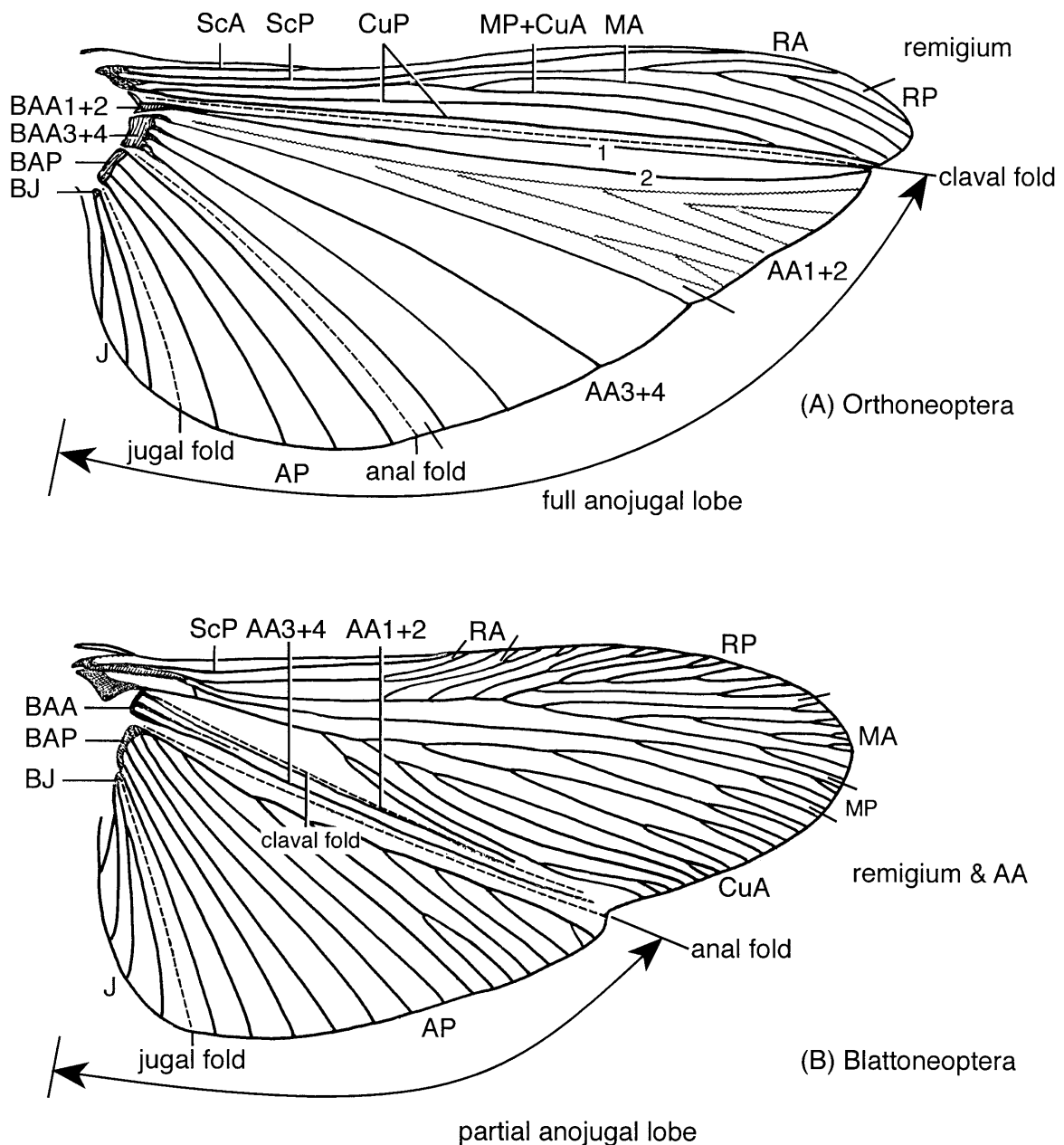
Fig. 21. The two types of neopteran anojugal lobes in hindwings. A – in Pleconeoptera and Orthoneoptera, the full anojugal lobe includes all pterygote branches: AA1+2, AA3+4, AP1+2, AP3+4, JA1+2, JA3+4, JP1+2, JP3+4; B – in Blattoneoptera, Hemineoptera and Endoneoptera the partial anojugal lobe starts at the anal fold and includes only AP and J branches; A – Orthoptera: Caelifera: *Valanga irregularis*; B – Blattodea: *Periplaneta americana*.

basivenalia: Cubital (BCu), anal (BAA3+4), and jugal (BJ). The pull of the wing flexor on the goblet makes the 3Ax body pivot, rotate and collapse into the membranized area vacated by the desclerotized PRCu, while the arms pull at the basivenalia and simultaneously fold the anojugal lobe backwards and over the abdomen. Deviations from this generalized pattern provide numerous important character states, at many taxonomic levels. As an example, Hemineoptera + Endoneoptera have anal arm (FA) fused with 3Ax saucer and protruding to articulate with BAA3+4 (Fig. 16); in coleopteroids + neuropteroids, FA changed into a narrow rim on the saucer, and the

articulation with BAA3+4 was replaced by several narrow strips of stiffened membrane (Fig. 17).

PHYLOGENETIC ANALYSIS OF THE EXTANT DERMAPTERA

Examination of the wing venation and articulation added 18 new characters to the previously existing data set (Haas, 1995). Also, more species have become available to re-assess the previously used characters and their states. Most of the character states recognized for dermapteran taxa were confirmed, and only a few character states had to be changed. Some of the previously used terms are replaced here by more precise terms. All changes are indicated and included in Table 4.

(A) Pleconeoptera
Orthoneoptera

(B) Blattoneoptera
Hemineoptera
Endoneoptera
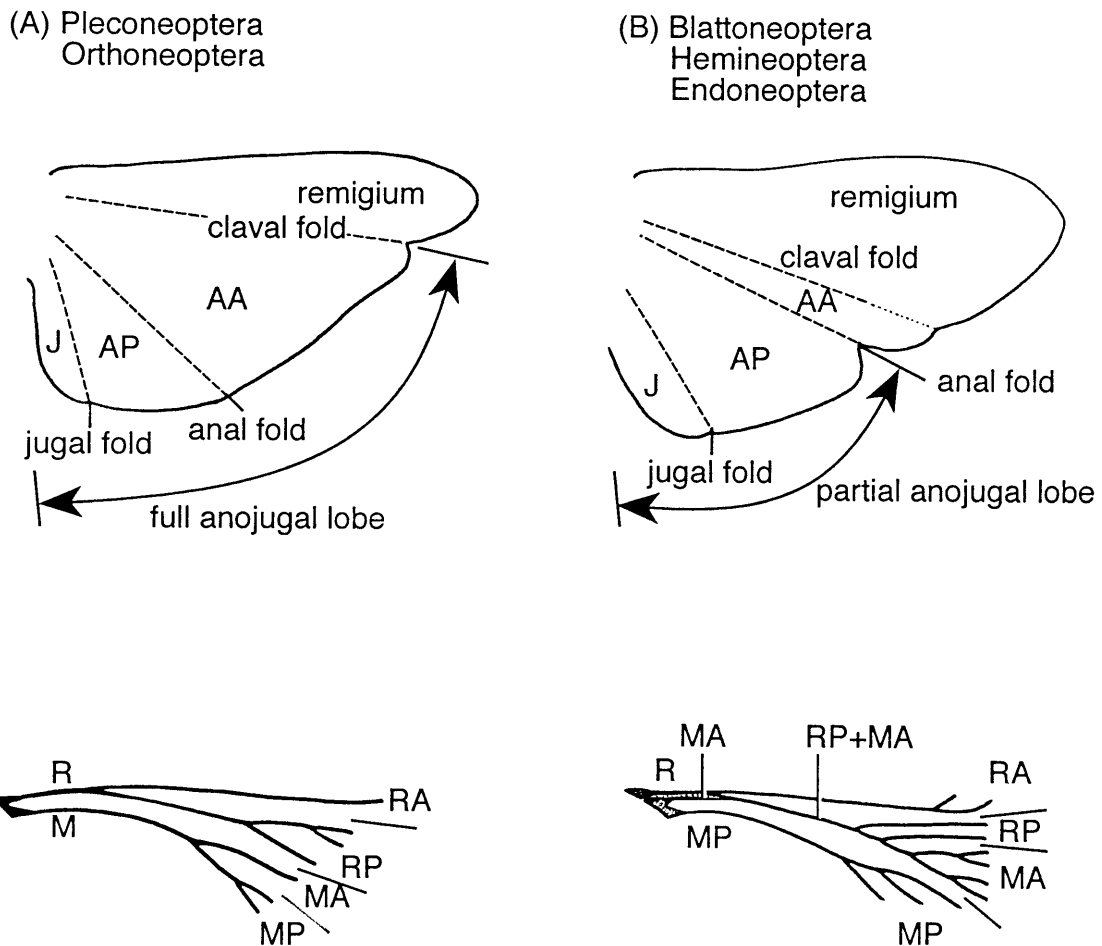
Fig. 22. Two fundamental flight adaptations in neopteran hindwing. A – in Pleconeoptera and Orthoneoptera, the anojugal lobe supported by AA, AP and J branches is separated from the remigium by a concave claval fold / flexion line; B – in Blattoneoptera, Hemineoptera and Endoneoptera the anojugal lobe contains only AP and J branches; AA area is combined with remigium into a special, extended flight unit separated from the diminished anojugal lobe by the anal fold.

Characters and their states

Hindwing and wing articulation

1. Fustis, shape. Head narrow, slender and elongate (0) or head broad, disc-like (1) (Fig. 4). The fustis head is narrow, slender and elongate in "Diplatyidae"; it is broad

and disk-like in the other taxa. The character is not applicable to the Blattodea and Karschiellidae.

2. Fustis, anterior margin. Smooth, without embayment (0) or with embayment (1) or with a notch (2) (Fig. 4). The fustis anterior margin is smooth and without embayment in the "Diplatyidae" and "Pygidicranidae";
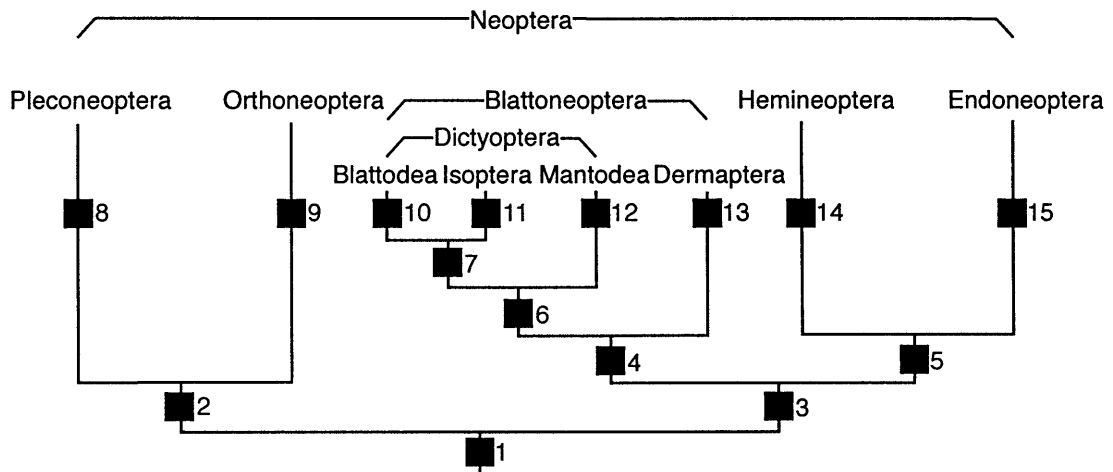
Fig. 23. Phylogenetic relationships of the Neoptera.

with an embayment in the "Labiduridae", Anisolabididae, Apachyidae and *Allostethus indicum*; with a notch only in the Spongiphoridae, Chelisochidae and Forficulidae. This character is not applicable to the Blattodea and Karschiellidae.

3. Fustis, head. Not separated (0) or separated (1) by a groove from the fustis base (Fig. 4). The fustis head is separated by a groove only in the Spongiphoridae, Chelisochidae and Forficulidae. This character is not applicable to the Blattodea and Karschiellidae.

4. Costal area. Long and slender (0) or short and broad (1) or long and broad (2) (Haas, 1995) (Fig. 4). The costal area is long and slender in the "Diplatyidae", short and broad in the "Pygidicranidae"; and long and broad in the remaining taxa.

This character replaces the formerly used character "marginal area" (Haas, 1995), because examination of additional species indicates that the distinction between "present" and "absent" cannot be upheld, and a more detailed distinction is possible now. This character is not applicable to Blattodea and Karschiellidae.

5. End of CuA3+4. Between the 8th and 9th branch of AP1+2 (0) or between 7th and 8th AP1+2 (1) or between 6th and 7th AP1+2 (2) or between 5th and 6th AP1+2 (3). The distal end of CuA3+4 lies between the 8th and 9th branch of AP1+2 in the "Diplatyidae" and Apachyidae; it lies between the 7th and 8th AP1+2 branch in *Allostethus indicum*, the Anisolabididae and "Pygidicranidae"; it lies between the 6th and 7th AP1+2 in the "Labiduridae" and Forficulidae; and it lies between the 5th and 6th AP1+2 branch only in the Spongiphoridae and Chelisochidae. This character is not applicable to the Blattodea and Karschiellidae.

6. Size of jugal and anojugal cells. About equal (0) or anojugal cell larger than jugal cell (1) or anojugal cell smaller than jugal cell (2) (Figs 5, 6). Both cells are of equal size in the "Diplatyidae", "Pygidicranidae" and Anisolabididae. The anojugal cell is larger than the jugal cell in all "Labiduridae", Spongiphoridae, Chelisochidae and Forficulidae; the anojugal cell is smaller than the jugal cell in the Apachyidae. This character is not applicable to the Blattodea and Karschiellidae.

7. Bending zones of the AP1+2 branches. At the base (0) or far from the base (1) or close to the base (2) (Figs 5, 6). The bending zones of the AP1+2 branches are located at the base in "Diplatyidae", "Pygidicranidae", Spongiphoridae, Forficulidae and Cheliosochidae; they occur at a small distance from the base in all "Labiduridae" and Anisolabididae; they occur at a great distance from the base only in Apachyidae. This character is not applicable to the Blattodea and Karschiellidae.

8. Position of rfc. At jugal cell (0) or forming a complete arch (1) or in between jugal and anojugal cell (2) or "U"-shaped (3) (Figs 5, 6). The ring fold cross-vein rfc is attached directly to the anojugal cell in the "Diplatyidae", "Pygidicranidae" and Apachyidae. It forms a complete arc in the "Labiduridae" (except *Allostethus indicum*). It lies between the jugal and anojugal cell in the Forficulidae. It is "U"-shaped in Chelisochidae and Forficulidae.

This character is not applicable to Blattodea and Karschiellidae.

9. Course of AP4. Angular, indented at ring fold (0) or sinusoidal at ring fold (1) (Figs 5, 6). The curvature of the AP4 is sinusoidal in the Spongiphoridae, Chelisochidae and Forficulidae. This character is not applicable to Blattodea and Karschiellidae.

10. AP4, ap3-ap4, exc1 and exc2. "Y"-shaped (0) or "H"-shaped (1) or buttressed "H"-shaped (2). Haas (1995) and (Figs 5, 6). This composite of veinal portions is "Y"-shaped in the "Diplatyidae", "Pygidicranidae" and *Allostethus indicum*, and "H"-shaped in the Apachyidae, "Labiduridae" and Forficulidae. The buttressed "H" appears only in the Chelisochidae and Spongiphoridae. This character is not applicable to Blattodea and Karschiellidae.

Closer examination showed that the former distinction between two character states was insufficient. Besides the "Y"-shaped situation, there are two other states and not only one ("4"-shaped), as assumed before (Haas, 1995). In each of the new states, a small cross vein is added.

11. End of JA3+4 and two proximal rc cross veins. Fully aligned and straight (0) or zigzag patterned (1) (Figs 5, 6). The JA3+4 and rc are fully aligned and straight in "Labiduridae" (excluding *Allostethus indicum*), Chelisochidae, Forficulidae and Spongiphoridae. They form a zigzag pattern in all other taxa examined. This character is not applicable to Blattodea and Karschiellidae.

12. JP3+4. The veinal portion posterior to rc, present (0) or absent (1) (Figs 5, 6). The posterior portion of JP3+4 is absent in the Anisolabididae, Chelisochidae, Spongiphoridae and Forficulidae; it is present in all other taxa examined. This character is not applicable to Blattodea and Karschiellidae.

13. 9th intercalary branch (between AA3 and AA4). Forked (0) or simple (1) (Figs 5, 6). This vein is forked in the "Diplatyidae", "Pygidicranidae", *Allostethus indicum*, "Labiduridae" and in Anisolabididae; it is simple in all other taxa. This character is not applicable to the Blattodea and Karschiellidae.

14. 3Ax saucer, jugal prong. Large (0) or small (1) to absent (2) (Figs 7–10). Jugal prong is pronounced in the "Diplatyidae", "Pygidicranidae" except *Tagalina burri*, and in *Allostethus indicum*; it is small in the Apachyidae, Anisolabididae, and absent in the "Labiduridae", Forficulidae, Chelisochidae and Spongiphoridae.

15. Anojugal arm FAJ, head. Almost elliptical (0) or narrow and very long (1) or narrow, undulated and short (2) (Figs 7–10). The head of FAJ is almost elliptical with a narrow neck posteriorly in the "Diplatyidae", "Pygidicranidae" and *Allostethus indicum*; narrow and very long in the Apachyidae, "Labiduridae" and Anisolabididae; and short, narrow and undulated in the Forficulidae, Spongiphoridae, and Chelisochidae. This character is not applicable to Blattodea and Karschiellidae.

16. Anojugal arm FAJ, neck and tail. Neck narrow, tail broad and weakly sclerotized (0) or neck broad, tail narrow and strongly sclerotized (1) (Figs 7–10). The neck

is narrow, the tail broad and weakly sclerotized in the "Diplatyidae", "Pygidicranidae" and *Allostethus indicum*; the neck is broad and the tail narrow in all other examined taxa. This character is not applicable to the Blattodea and Karschiellidae.

17. Anojugal arm FAJ, tail. Posterior part of tail concave and strongly three-dimensional (0) or flat (1) (Figs 7–10). FAJ is strongly three dimensional only in the "Diplatyidae"; it is flat in all other taxa. The character is not applicable to Blattodea and Karschiellidae.

18. Combined basivenalia BAA3+4, BAP, BJ. Not or slightly twisted (0) or strongly twisted (1) (Figs 7–10). Basivenalia BAA3+4, BAP, BJ are not or only slightly twisted in the "Diplatyidae", "Pygidicranidae", Apachyidae and *Allostethus indicum*. They are strongly twisted in the other taxa examined. This character is not applicable to Blattodea and Karschiellidae.

19. Position of AA3. Far from BAA1+2 (0) or close to BAA1+2 (1), Haas (1995) and (Figs 7–10). The AA3 diverges far distally from BAA1+2 in the "Diplatyidae", "Pygidicranidae" and *Allostethus indicum*. The AA3 diverges close to BAA1+2 in the other taxa.

This character was formerly called "a cross vein: in front of or after bend" (Haas, 1995), which is a non-homologous term. The homologized terminology is now employed, but no changes in the character assessment were necessary. This character is not applicable to Blattodea and Karschiellidae.

20. Anal window, closure. Window closes proximal to AA3 (0) or distal to AA3 (1) or window is open (2) (Figs 7-10). Anal window is formed by a divergence and a subsequent fusion, of AA3+4 and AP; it closes proximally to the base of AA3 in the "Diplatyidae" and "Pygidicranidae"; it closes distally to the base of AA3 in *Allostethus indicum*, Apachyidae, Anisolabididae and "Labiduridae". AP is membranized at the point of fusion with AA3 in the Forficulidae, Chelisochidae and Spongiphoridae. This character is not applicable to Blattodea and Karschiellidae.

21. CuP. Distinct (0) or indistinct (1) (Haas, 1995). The CuP is distinct in the Blattodea, "Diplatyidae" excluding *Diplatys gerstaeckeri*, "Pygidicranidae" and *Allostethus indicum*; CuP is indistinct in all other taxa examined (Figs 7–10).

CuP was previously called Cu2. The Apachyidae are now considered to have a short CuP. The character is not applicable to the wingless Karschiellidae.

22. Concave longitudinal fold (clf). Median (0) or lateral (1) (Haas, 1995). The clf runs almost medially between CuA and AP in the "Diplatyidae" and "Pygidicranidae"; it runs closer to AP in all other taxa (Figs 7–10). The clf is not present in Blattodea and Karschiellidae; the character is not applicable.

As pointed out below, the clf is a system of two or three folds. The functional term is used here for the combination of claval fold, anal fold and CuP.

23. Broadenings of radiating and intercalary branches. Connected (0) or separated (1) (Haas, 1995). The broadenings are separated only in the Chelisochidae,

Spongiphoridae and Forficulidae. This character is not applicable to the Blattodea and Karschiellidae.

The broadenings were formerly called "broadened areas". The examination showed that the distinction between the connected and separated broadenings is most evident in the first three to four pairs of radiating and intercalary branches; no changes in character states were necessary.

24. Branching of AP1+2. AP1+2 proximal branches diverge very close together (0) or are broadly separated (1) (Figs 5, 6). Two proximal branches of AP1+2 diverge close together in the "Diplatyidae"; they are well distanced in all other dermapteran taxa. AP1+2 branches are either pectinate or dichotomously branched in the Blattodea (Figs 11A, B); the character is not applicable to the Karschiellidae.

Thorax and tegmina

25. Tegmina. Symmetrical (0) or asymmetrical (1) (Haas, 1995). The tegmina are symmetrical only in the Blattodea, all examined species of *Haplodiplatys* and Karschiellidae. Apart from those taxa they are asymmetrical.

26. Metanotum. Flat (0) or with median longitudinal groove (1) (Haas, 1995). The metanotum is flat in the Blattodea and Karschiellidae; it has a median groove in all other examined Dermaptera.

27. Spiny crest on tegmina. Absent (0) or present (1) (Haas, 1995). The spiny crest is absent in Blattodea and Karschiellidae, but present in the other examined Dermaptera.

28. Spiny ridge on metanotum. Absent (0) or present (1) (Haas, 1995). The spiny ridge is absent in the Blattodea, Karschiellidae and all examined species of *Haplodiplatys*; it is present in all other examined Dermaptera.

The spiny ridge was formerly referred to as a tegminal locking device. This term is now considered to be inappropriate because the tegminal locking device consists of several structures not confined to the metanotum. The combination of structures described here as characters 25 to 28 form the tegminal locking device.

29. Mesonotal ratio. High, over 0.55 (0) or low, under 0.54 (1) (Haas, 1995). It is calculated as the ratio of mesonotal length divided by its width. A high ratio is found in Blattodea and all dermapteran taxa except the Chelisochidae, Spongiphoridae and Forficulidae, which have a low ratio.

The measurements for the Anisolabididae (Haas, 1995) were based on a single specimen of *Carcinophora americana*. More specimens have become available and the ratio was measured and calculated again. These new measurements (mean: 0.63; standard deviation: 0.03; sample size: 5) show that the situation in the Anisolabididae was formerly misinterpreted as low and that their mesonota have in fact a high ratio.

30. Median posterior tip. Lightly sclerotized and not pronounced (0) or heavily sclerotized and pronounced, well marked (1) (Haas, 1995). A lightly sclerotised and unpronounced tip is found in all examined Dermaptera except Chelisochidae, Forficulidae and Spongiphoridae,

which have a heavily sclerotised and pronounced tip. The character state for Anisolabididae was changed from 1 to 0 after more material became available (see character 29).

31. Cranial margin of tegmen. Curved (0) or straight (1) (Haas, 1995). The cranial margin is straight in the Chelisochidae, Forficulidae and Spongiphoridae; it is curved in the other examined Dermaptera and Blattodea. The character state for Anisolabididae is changed from 1 to 0 after more material became available (see character 29).

Neck, legs and abdomen

32. Neck. Blattoid-type (0) or forficuloid-type (1) (Haas, 1995). The Blattodea, Karschiellidae, "Diplatyidae" and "Pygidicranidae" posses a blattoid-type neck; all other examined Dermaptera possess a forficuloid-type neck.

33. Femur. Carinate (0) or rounded (1) (Haas, 1995). The femur is carinate in *Periplaneta americana*, Karschiellidae, "Diplatyidae", "Pygidicranidae" and Apachyidae. It is rounded in *Leucopheae maderae, Polyphaga aegyptiaca, Allostethus indicum,* "Labiduridae", Anisolabididae, Spongiphoridae, Chelisochidae and Forficulidae.

34. Number of tarsomeres. Five (0) or three (1) (Haas, 1995). All examined Dermaptera have tarsi with three tarsomeres, whereas the Blattodea have tarsi with five tarsomeres.

35. 2nd tarsomeres. Normal, not elongated (0) or long and slender (1) or heart-shaped (2) (Haas, 1995). All examined Blattodea and Dermaptera have normal, not elongated 2nd tarsomeres, except the Chelisochidae possessing a long and slender tarsomere and the Forficulidae possessing a cordiform 2nd tarsomere.

36. 10th abdominal segment. Normal (0) or dilated (1) (Haas, 1995). The 10th abdominal segment is normal in all taxa examined, except in the Apachyidae, which possess a dilated 10th abdominal segment.

37. Larval cerci. Annulated (0) or smooth, not annulated (1) (Haas, 1995). The larval cerci are annulated in Blattodea, Karschiellidae and "Diplatyidae". They are smooth and not annulated in all other Dermaptera examined.

38. Adult cerci. Annulated (0) or smooth, not annulated (1) (Haas, 1995). The adult cerci are annulated in Blattodea. They are smooth, not annulated in all Dermaptera examined.

39. Division of telson. Fused (0) or subdivided (1) (Haas, 1995). The telson or pygidium consists of three parts which are fused in the Apachyidae, *Allostethus indicum,* "Labiduridae", Anisolabididae, Chelisochidae, Forficulidae and Spongiphoridae.

40. Abdominal tergites and sternites. Abutting (0) or overlapping pleurally (1) (Giles, 1963; Rentz & Kevan, 1991; Roth, 1991). The abdominal tergites and sternites abut in Blattodea and overlap pleurally in all Dermaptera examined.

Male genitalia

41. Number and direction of genital lobes. Two genital lobes unidirected (0) or two genital lobes bidirected (1) or one genital lobe (2) or karschiellid-type (3) (Haas, 1995). The two genital lobes of "Diplatyidae" and "Pygidicranidae" are unidirected, whereas the two genital lobes of Apachyidae, *Allostethus indicum* and Anisolabididae are bidirected. The Spongiphoridae, Chelisochidae and Forficulidae possess only one genital lobe. The karschiellid-type penes is present exclusively in Karschiellidae. Due to the structure of the genitalia, this character is not applicable to the Blattodea.

42. Total number of virgae. One (0) or two (1) or four (2) (Haas, 1995). The Karschiellidae, Spongiphoridae, Chelisochidae and Forficulidae possess one virga. The "Pygidicranidae" except *Pyragra fuscata*, Apachyidae, "Labiduridae", *Allostethus indicum* and Anisolabididae possess two virgae. The "Diplatyidae" and *Pyragra fuscata* possess four virgae. This character is not applicable to Blattodea due to the structure of the genitalia.

43. Basal vesicle. Absent (0) or present (1) (Haas, 1995). The basal vesicle is absent in Karschiellidae, "Diplatyidae", "Pygidicranidae", Anisolabididae and Spongiphoridae. It is present in all other Dermaptera examined. This character is not applicable to Blattodea due to the structure of the genitalia.

Character analysis

The analysis of the data set (Table 4) results in four equally parsimonious trees with a tree length of 72, CI 0.819 and RI 0.935. Fig. 24A depicts the preferred tree. Ambiguous characters are marked with an asterisk (*).

The Karschiellidae come out as monophyletic (character 41). The "Diplatyidae" are not a subtaxon of the "Pygidicranidae" and appear to be paraphyletic. The monophyly of a taxon "Pygidicranidae" (excluding Karschiellidae and "Diplatyidae") is not supported. In contrast, all examined species of *Echinosoma* and *Tagalina burri* share an apomorphy (character 42) with the more derived taxa.

Allostethus indicum is usually placed in the "Labiduridae" (Brindle, 1965a; Steinmann, 1989) but appears to be more closely related to the "Pygidicranidae" and Apachyidae in our analyses. This is due to eight apomorphic character states in the "Labiduridae" in which *Allostethus indicum* shows the plesiomorphic character state (characters 5, 10, 11, 15, 16, 18, 19, 20). The Apachyidae appear to be monophyletic (characters 5, 6, 7, 13, 33*, 36), however only one species was examined. They are never a subtaxon of the "Labiduridae".

The monophyly of "Labiduridae" (excluding *Allostethus indicum* and Apachyidae) is not supported by strict consensus tree (not shown). However, in two of four trees they appear monophyletic (characters 8*, 12* as ambigous apomorphies). If monophyletic, they are always the sistergroup to the Eudermaptera (Spongiphoridae + Chelisochidae + Forficulidae).

The Eudermaptera are monophyletic, and there are 14 characters to support this view (characters 2, 3, 7, 9, 12*,

13, 15, 20, 23, 29, 30, 31, 41, 42). A sistergroup relationship of the Chelisochidae and Spongiphoridae is suggested by characters 5, 8* and 10. The Spongiphoridae are probably monophyletic (character 43 state 0) The Chelisochidae are probably monophyletic (character 35 state 1). The Forficulidae are probably monophyletic (character 8*, 35 state 2).

PHYLOGENETIC ANALYSIS OF FOSSIL DERMAPTERA

A close relationship between Dermaptera and "Protelytroptera", or a sub-group of the latter, has often been assumed (Tillyard, 1931; Hennig, 1969, 1981; Boudreaux, 1979; Kukalová-Peck, 1991; Carpenter, 1992). However, no cladistic analysis has been conducted so far. We present a cladistic analysis for this relationship including *Protelytron permianum* (Fig. 19), *Acosmelytron delicatum* (Fig. 18) and *Apachelytron transversum* (Fig. 3). This selection was made because all other species of "Protelytroptera" are only known by their tegmina and show no wing folding, wing venation, or body characters (Carpenter, 1992).

Apachelytron transversum (Fig. 3) shares with extant Dermaptera many autapomorphies in the wing venation: Veinal sector MP long and simple for most of its course; arculus (mp-cua) present; the stem of Cu relatively long; CuA branches end on anal vein instead of reaching posterior margin; CuP short, directed towards and ending on anal vein; AA1+2 completely lost (remnants present in other Blattoneoptera); and AP1+2 sending off a series (8 to 10) of pectinate branches. These characters are not included below because they are not available either in the other "Protelytroptera" or in fossil Dermaptera.

Characters and their states

In order to avoid ambiguities, the character numbers continue below with 44. *Apachelytron transversum* shares derived characters in the wing venation with the Dermaptera, *Protelytron permianum* and *Acosmelytron delicatum* and, therefore, it is included in the analysis below.

44. Number of ocelli. Two (0) or none (1). All examined taxa apart from *Diplatys jacobsoni* have two ocelli.

45. Head. Opisthognathous (0) or prognathous (1). *Periplaneta americana* has an opisthognathous head, while all other examined taxa possess a prognathous head. The character state is not known in *Acosmelytron delicatum* and *Apachelytron transversum*.

46. Pronotum. Disc-like, large, Blattodea-type (0) or disc-like, small, Dermaptera-type (1). The disc-like pronotum is small in fossil and extant Dermaptera, while being large in *Periplaneta americana*. The character state is not known in *Acosmelytron delicatum* and *Apachelytron transversum* due to poor preservation.

47. Spines on femoral carina. Present (0) or absent (1). Spines are present in *Diplatys jacobsoni, Archidermapteron martynovi, Asiodiplatys speciosus, Microdiplatys campodeiformis* and *Protodiplatys fortis*. They are absent in all other examined taxa.

48. Number of tarsomeres. Five (0) or three (1). There are tarsi with three tarsomeres in *Diplatys jacobsoni, Semenoviola obliquotruncata, Semenovioloides capitatus*

and *Turanoderma sepultum*. All other examined taxa have tarsi with five tarsomeres.

49. Hindwing. Long, folded fan-like (0) or with one transverse fold (1) or with two transverse folds (2), wing package. A wing package with two transverse folds is present in all fossil and extant Dermaptera. Amongst the examined "Protelytroptera", *Protelytron permianum*, has a wing with one transverse fold. All other examined taxa have a simple fan-wise folded wing.

50. Broadenings. Absent (0) or present (1). The broadenings are present in all fossil and extant Dermaptera and *Protelytron permianum*. They are absent in all other examined taxa.

51. Tergites and sternites overlapping in abdominal segments. Not overlapping (0) or overlapping (1). These plates are overlapping in all fossil and extant Dermaptera and *Acosmelytron delicatum*. The characters state is not known in *Apachelytron transversum* and *Protelytron permianum* due to poor preservation. There is no overlap in the tergites and sternites of *Periplaneta americana*.

52. 8th and 9th abdominal tergite in females. Distinct and separate from 10th tergite (0) or narrowed, but separate from 10th tergite and not covered by 7th tergite (1) or fused to 10th tergite and covered by 7th (2). The tergites are distinct and separate in *Periplaneta americana, Acosmelytron delicatum, Apachelytron transversum, Archidermapteron martynovi, Asiodiplatys speciousus, Dermapteron incertae, Microdiplatys campodeiformes, Protodiplatys fortis* and *Turanovia incompleta*. The tergites are narrowed in *Semenoviola obliquotruncata, Semenovioloides capitatus, Turanoderma sepultum* and fused only in *Diplatys jacobsoni*.

53. Ovipositor. Straight, long (0) or short or absent (1). Character state 1 is found in *Diplatys jacobsoni, Dermapteron incertae, Semenoviola obliquotruncata, Semenovioloides capitatus, Turanoderma sepultum* and *Turanovia incompleta*. Character state 0 is found in all other examined taxa, except in *Acosmelytron delicatum, Protelytron permianum, Archaeosoma serratum* and *Longiceratus mesozoica* due to poor preservation or because the specimen is a male.

54. Adult cerci. Annulated, short (0) or annulated, long (1) or annulated, but basal article is much larger than others (2) or smooth (3). Smooth cerci are present in *Diplatys jacobsoni* and *Archaeosoma serratum, Semenoviola obliquotruncata, Semenovioloides capitatus, Turanoderma sepultum*. They are annulated and long in *Archidermapteron martynovi, Asiodiplatys speciousus, Longiceratus mesozoica, Microdiplatys campodeiformis* and *Protodiplatys fortis*. The basal article is much larger than the following ones only in *Dermapteron incertae* and *Turanovia incompleta*. The adult cerci are annulated and short in *Periplaneta americana, Acosmelytron delicatum* and *Apachelytron transversum*. The character state of *Protelytron permianum* is not known due to poor preservation.

Character analysis

The analysis of the data set (Table 5) results in 588 equally short trees with tree length 15, CI 1.0 and RI 1.0.

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The preferred tree is shown in Fig. 24B. The high number of taxa together with the low number of characters results in a large number of equally short trees. However, there is some resolution in the preferred tree.

Apachelytron transversum does not differ in characters given in the matrix from the Blattodea *Periplaneta americana*. However, it is included in the ingroup on the grounds given above. *Protelytron permianum* shares two
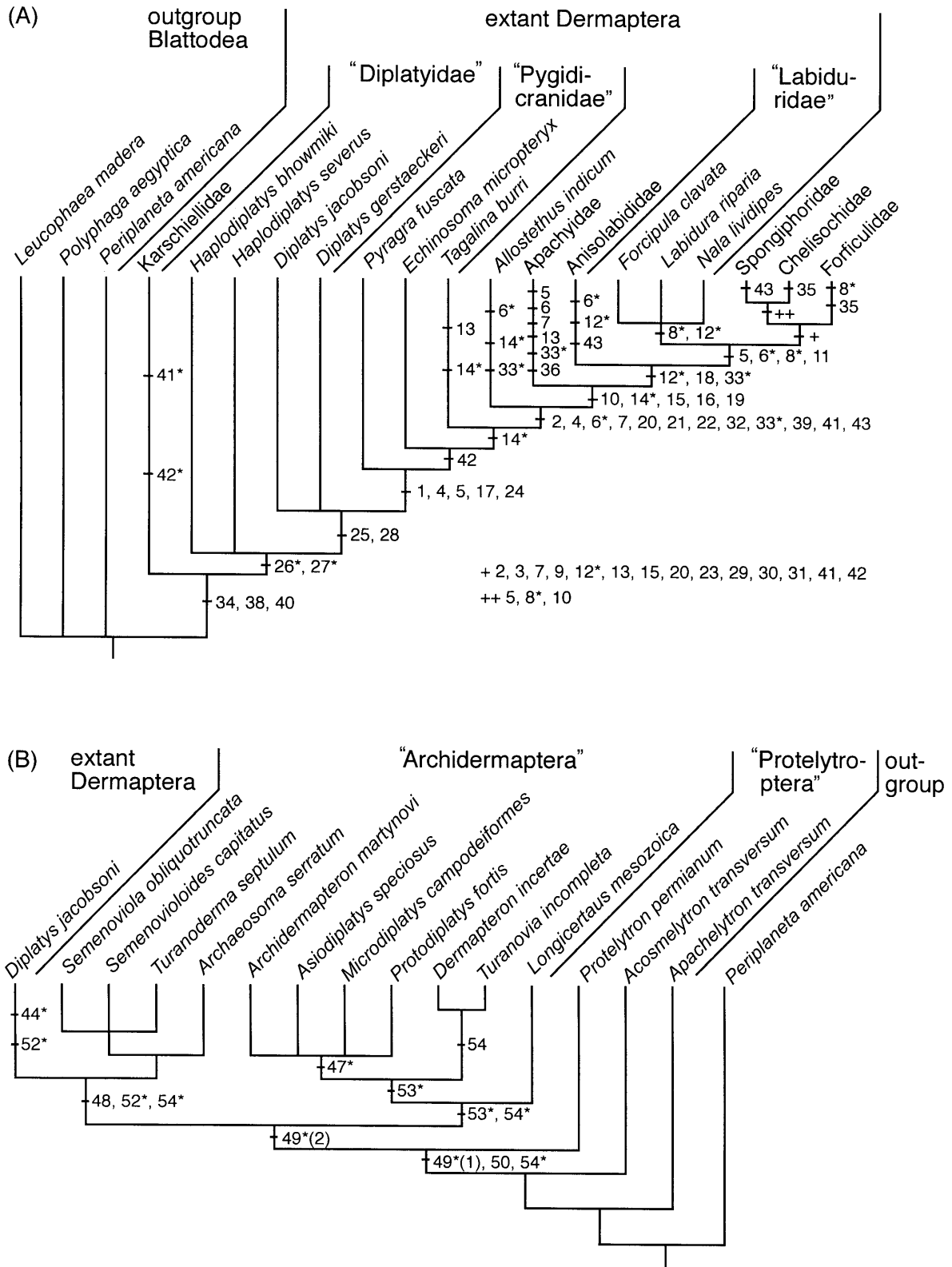

Fig. 24. A – the preferred tree of four equally parsimonious trees with tree length 72, CI 0.819 and RI 0.935, showing the relationships of extant Dermaptera; B – the preferred tree of 588 equally parsimonious trees with length 15, CI 1.0 and RI 1.0, showing the relationships of fossil and extant Dermaptera to their stem line. Asterisk (*) – ambiguous characters.

derived wing characters (characters 49, 50) with the higher fossil Dermaptera.

The "Archidermaptera", comprising the genera *Semenoviola*, *Semenovioloides*, *Turanoderma*, *Protodiplatys*, *Archidermapteron*, *Asiodiplatys*, *Dermapteron*, *Microdiplatys*, *Turanovia*, *Archaeosoma*, and *Longiceratus* are paraphyletic and they are not the sistergroup of extant Dermaptera, represented by *Diplatys jacobsoni*.

The monophyletic taxon within the "Archidermaptera", comprising the genera *Protodiplatys*, *Archidermapteron*, *Asiodiplatys* and *Microdiplatys*, shares the possession of spines on the femoral carina (characters 47). The genera *Dermapteron* and *Turanovia* share the type of cerci (character 54).

Extant Dermaptera constitute a monophyletic taxon, sharing the reduction of ocelli and the fusion of the 8th and 9th abdominal female tergite to the 10th tergite, including a covering of the former by the 7th tergite (characters 44, 52).

DISCUSSION

As documented above and in the characters in Table 6, transformations in the ground patterns of the wing complex proceed step-wise from the Pterygota protowing, to Neoptera, to Blattoneoptera, to Dermaptera and finally to the dermapteran families. We are convinced that the phylogenetic relationships of any pterygote order, and especially of Dermaptera (because of their highly unusual wing pattern), can be seen only in the broad evolutionary context of all other pterygote orders. As an example, to show that the prominent anojugal lobe in Dermaptera is typically blattoid rather than endopterygote or orthopteroid, it is first necessary to document the diversification of all three lobes from the shared Neoptera ground pattern. This can be recognized only after distinguishing it from its homologue in the ex-group, the palaeopterous ground pattern. The palaeopterous lobe must be interpreted by research on all palaeopterous orders. Finally, both neopterous and palaeopterous anojugal lobes must be fully homologized, i.e., must be derived from a single, shared pterygote protowing pattern (Table 6: Introduction). Thus, preparing in a pterygote order a wing ground pattern for higher phylogenetic analysis, snowballs instantly and inevitably into a need to know the ground patterns of all other pterygote orders.

In a quest for presenting results based on sufficient documentation, we had no other choice but to trace all step-wise changes in wing character states, from the protowing to Dermaptera. Furthermore, dermapteran wings are so unusually altered that to show clearly their underlaying blattoid pattern, they had to be studied in conjunction with a detailed functional analysis.

The most difficult hurdle to be overcome in using the wing complex in higher phylogenetics is dealing with the fact that the apomorphies are largely limited to reductions and fusions. Veins and articular sclerites are getting constantly fused or reduced at all systematic levels. Thus, the synapomorphies usually cannot be empirically distinguished if inspected as separate characters. However, in spite of this problem, the underlying ground pattern usually instantly identifies each wing and articulation as a particular order or family. This dilemma suggests that to avoid problems with homoplasies, it is necessary to keep the integrated ground pattern characters together. It is essential to compare one wing ground pattern with another wing ground patterns, and to avoid completely comparing one separate (neopterous) character with another separate (neopterous) character. The way to recognize synapomorphies is to search for them within the context of their ground pattern. In other words, the stepwise transformations in integrated character complexes, which separate one ground pattern from another, also show the phylogenetic relationships. We are convinced that this method is repeatable and, therefore, an objective method of character assessment in higher phylogenetics.

Our illustration of this method in Table 6 shows the amazing number of homoplasies that accompany and parallel almost every wing synapomorphy. Under these circumstances, we consider selecting and assessing the higher-level wing characters as separate entities (i.e., outside the context of their particular ground pattern and without full homologization with the other ground patterns) as a haphazard and unreliable method. Note that under the circumstances, subsequent processing simply cannot improve the quality of the basal data set. Countless morphologically unsupportable higher phylogenetic schemes result.

As background to the wing data set in Table 6, we are offering here a brief overview of the main phylogenetic events, which lead to the Dermaptera. The events correspond to the main nodi in the phylogenetic tree on Fig. 23.

Pterygota: Protowing and the split into Palaeoptera and Neoptera

Pterygota are monophyletic and all wing characters (venation and articulation) evolved from a single protowing ground pattern. Morphological evidence indicates that ancestral pterygotes had three pairs of small, movable, articulated protowings that were incapable of powered aerial flight, but almost certainly were flapping and generating some kind of forward movement. Only the prothoracic pair of protowings is recorded in fossils. They were retained in a partly immobilized and slightly reduced condition in the adults of Carboniferous Palaeodictyoptera and Geroptera (odonatoid stem line). Three pairs of small, homonomous, mobile wings were present in the nymphs of the plesiomorphic palaeopterous Diaphanopterodea. These nymphal wings could be simply folded (warped) and pulled towards the body, in a way that quite probably occurred in oldest protowings (Brodsky, 1994; Kukalová-Peck, 1978, 1983, 1991, 1997; Willmann, 1997; Wootton & Kukalová-Peck, 2000) (Table 6).

The fundamental split of the Pterygota into Palaeoptera and Neoptera (Martynov, 1923) probably took place when the three pairs of protowings were homonomous, their venation was radially arranged, there were no folds, and the wing veins lacked fusions and braces. Some of these features are retained only in Palaeoptera, others

only in Neoptera. Fusions and braces are crucial for powered forward fligh. Without exception, they occur in all wings capable of powered flapping flight; insects with highly reduced venation are very small and depend on air currents. Therefore, the absence of shared fusions and braces in Neoptera shows that the neopterous ancestor could not fly in the air. In other words, flapping aerial flight is not a neopterous (or pterygote) synapomorphy. Lack of the shared flight adaptation in Neoptera is consistent with the fact that Neoptera and Palaeoptera have fundamentally different wing pair symmetry, costal margin, anojugal lobes, veinal fusions, veinal braces, and arrangement of the wing articulation (Fig. 1A, B). In Table 6A, an astonishing 65 different wing characters are listed in the ground pattern of Palaeoptera and Neoptera. Pterygote protowing is shared by all Pterygota but the functional adaptations, which converted the flapping appendage to an aerial flying appendage, evolved in several directions. Like in aeroplanes, there is a multiplicity of forms and patterns that can become flight-worthy.

Palaeoptera bear forewings and hindwings which are homonomous in size, contain a radially arranged and regularly corrugated wing venation, are membranous, and with a strong irregular inter-veinal network. The remigium, anal lobe and jugal lobe are all at one plane. The jugal area is always strongly reduced. There are no shared stabilized wing folds between wing areas. Two veinal stems are always present, the medial and cubital. The radial stem in modern Ephemeroptera and Odonatoptera has RA & RP fused side-by-side (in the radial stem of Neoptera, RA & RP are always superimposed). The sclerites in the palaeopterous wing articulation are always arranged in regular rows and columns and are positioned close together (clustered) centrally near the wing base (Kukalová-Peck & Brauckmann, 1990). This arrangement is predisposed for an easy fusion between fulcalaria (F) sclerites on the body side and basivenalia (B) sclerites on the wing side. The resulting articular plate rests on the pleural wall and creates a lever rocking on the pleural fulcrum point. But, the wings become fixed in a permanently outstretched position, are incapable of being flexed backward over the abdomen, and prevent escape from predators by hiding in narrow spaces. In exchange, the insect can glide effortlessly with minimum energy expenditure, and may "outgrow" predators by gigantic increase in size. Mayflies and damselflies can hold their wings lifted upwards when at rest. Only a single, most primitive fossil order, the Diaphanopterodea, retained the ancestral ability to flex their wings backward over the abdomen. In the rest of Palaeoptera the fusion of centrally positioned sclerites into an articular plate happened twice differently: (i) in Palaeodictyoptera + Megasecoptera, and again (ii) in Ephemeroptera + Odonatoptera (Kukalová-Peck, 1985, 1997; in progress). All Palaeoptera have fragile membranous forewings and hindwings. The data above indicate that the early survival tactics in Palaeoptera was not hiding from predators, but rather flying away. The resulting speedy and highly sophisticated perfection of flight is richly documented in the Palaeozoic fossil record (Wootton & Kukalová-Peck, 2000, and for references).

Neoptera bear in their ground pattern a pair of fore and hindwing, which are heteronomous in appearance, size and function. The forewings are tegminous, narrower and thicker than the hindwings. They participate in flight and protect the hindwings, which are the main flying pair (Brodsky, 1994). In forewings, the remigium and anal lobe are at one plane, but the jugal lobe is at another plane. The jugal lobe is membranized, strongly reduced and is folded under the anal lobe. Anal lobe bears a long, strong anal bar composed of BAA + BAP, adapted to locking the wing at rest. Anal branches are not radially arranged, but are distributed irregularly. Principal branch AA1+2 is distanced from AA3+4, and AA3+4 is always fused basally with AP.

The hindwings are much broader than the forewings, are membranous, with a sparse inter-veinal network, and bear plesiotypic radially arranged veins as in Palaeoptera. The anal lobe and jugal lobe are at the same plane. Both wing pairs have four stabilized folds: Medial, claval, anal and jugal. They share an anal brace between BAA and BCu engaged in wing flexing. The veinal corrugation (convex: +, and concave: –) is permanent in the veins ScA+, ScP– and RA+, but the remaining veins have a variable corrugation (convexity and concavity is often diminished or even reversed) (Fig. 1).

Neopterous wing articulation is typical and unique, and it presents Neoptera as a convincingly monophyletic group. The asymetrical composite sclerites 1Ax and 2Ax, and the rotating composite sclerite 3Ax (Fig. 1) are designed for flexing of the wings backward and locking them securely in a flexed position. The characters most informative in higher phylogenetics occur in 3Ax (goblet + saucer) and its arms, 2Ax body and arm, subcostal basivenale BSc, PWP, and in the veinal basivenalia. The same features are highly autapomorphic in Dermaptera. As an important fact, Neoptera share a highly efficient flexing mechanism, but do not share any veinal stems and braces necessary for aerial powered flight. This is consistent with the neopterous ancestor whose main survival strategy was probably flexing the wings backward and hiding from predators in narrow spaces, while flight seems to have been initially of a somewhat lesser importance. Indeed, the high manoeuverability of wings and high speed in flight comparable to those in Carboniferous Odonata and Megasecoptera (Wootton & Kukalová-Peck, 2000) came to the Neoptera only in the Mesozoic, in Diptera and some Hymenoptera. The most informative higher level characters in neopterous venation occur in veinal stems and braces near the wing base (Table 6B–H).

In the Neoptera ground pattern, the forewing is protective as well as flying. But, the main flying wing is the hindwing with an enlarged anojugal lobe (Brodsky, 1994). This concept, which is originally based on functional analysis of the flight motor, is confirmed here by wing articulation. The neopterous hindwing ground pattern includes a triple subdivision of the anal basivenale, to accommodate the many veins needed to support the

enlarged anojugal lobe. Neopterous anal basivenale BA (=the sclerotized blood sinus of anal branches) is subdivided into three mutually articulated sections (BAA1+2, BAA3+4, BAP: Figs 1, 11–17), which service numerous anal branches supporting the enlarged anal lobe. This triple subdivision is absent in the Palaeoptera, well pronounced in the lower Neoptera and is present or indicated in the higher Neoptera even when the anal lobe was reduced (see Figs 11–17; Table 6). The enlarged lobe occurs in plesiomorphic Pleconeoptera, Orthoneoptera and Blattoneoptera, in some basal representatives of Hemineoptera (Fulgoromorpha, some Auchenorrhyncha) and of Endoneoptera (Hymenoptera: Xyelidae, Coleoptera, Megaloptera, Ithonidae (Neuroptera), Philopotamidae (Trichoptera). Later changes in the anojugal lobe include further secondary enlargement (e.g., in Dermaptera), abrupt reduction (in petiolate wings), and gradual reduction (in Hemineoptera, Endoneoptera). The changes occur independently, randomly and in parallel, simultaneously at the superorder, order, suborder and family level, and are responsible for many homoplasies. In Pleconeoptera, the basal anojugal lobe was initially large and then diminished – gradually in derived Plecoptera and abruptly in Embioptera. In Orthoneoptera, the prevalent tendency was to retain and further enlarge the anojugal lobe and to add secondary anal branches. In Blattoneoptera (including Dermaptera) the AA area is combined with the remigium, and removed from the partial anal lobe. But, the remaining AP + J areas became enlarged, and AP developed secondary anal branches to fill up the new space. In Hemineoptera and Endoneoptera the AA area is also removed, but instead of compensating for the loss, the entire hindwing started to diminish and the anojugal lobe lost even more anal branches, and the forewings became the main flying pair.

An important fact is that Neoptera share all articular sclerites, but do not share any veinal stems or braces near the wing base, which are crucial for aerial powered flight. This indicates that the wing flexing evolved before these adaptations were established in the neopterous ground pattern. There are two different patterns of fusions and braces important in aerial flight, but neither can be ancestral to the other: In Pleconeoptera + Orthoneoptera and in Blattoneoptera + (Hemineoptera + Endoneoptera). The differences include: (1) fusions and braces of the medial vein; (2) composition of the anojugal lobe; (3) composition of the flight units; and (4) the use of the flight-important folds. Brodsky (1994) proposed that both groups also independently evolved two types of flight motor. These two patterns probably evolved from a common ancestor (as summarized here in Figs 22, 23) and represent sistergroups.

Neoptera: Basal split into Pleconeoptera + Orthoneoptera and Blattoneoptera + Hemineoptera + Endoneoptera

The most profound morphological difference between the two basal groups of Neoptera is in the composition of the anojugal lobe. This lobe is particularly important in flight. Pleconeoptera (Fig. 14) and Orthoneoptera (Fig.

15) have a **full anojugal lobe**, which starts at the claval fold (the main flexion line in flight) and contains two anal and two jugal sectors (AA, AP, JA, JP), a symplesiomorphy (Figs 21, 22). The remigium represents a **flight unit** of its own (Table 6B). Contrary to this, Blattoneoptera, Hemineoptera and Endoneoptera share a **partial anojugal lobe**, which starts at the anal fold and contains only one anal and two jugal sectors (AP, JA, JP) (Figs 11, 12, 13, 17, 21, 22). The anterior anal sector (AA) is progressively reduced and combined with the remigium into a **composite flight unit**, an autapomorphy (Figs 20, 21B, 17) (Table 6D). The claval fold, which lost its function as the main flexion line, is gradually reduced, first shallower, then shorter or lost. The anal fold became the main flexing fold (an autapomorphy). It separates the partial anojugal lobe, which is supported only by the branches of AP and J. Further splitting occurs as follows.

In **Blattoneoptera** the original main flying role of the hindwings is sustained in spite of the partial anojugal lobe. This is possible by adding some autapomorphies. Diminished veinal support is compensated for by the secondary terminal branches, which are added to AP1+2. This phenomenon is especially well pronounced in **Dermaptera** and in related **Dictyoptera** (see Table 6E). In contrast, partial anojugal lobe in **Hemineoptera + Endoneoptera** gradually becomes smaller and anal branches shorter and more impoverished. Eventually, most endoneopterous hind wings end up being smaller than the forewings, their role in flight is reversed, and forewings become the main flying pair. Sometimes the fore- and hindwing hook together and are used as a single flying wing. Even this complex flight adaptation is a homoplasy, occurring in parallel in Hemiptera, Hymenoptera, and Lepidoptera.

The morphological split of the anojugal lobe into two types accompanies an equally important split of the braces in the medial vein into two types. In **Orthoneoptera + Pleconeoptera** the medial sectors MA and MP fuse basally into a long stem of M (a synapomorphy) and medial branches belong to both MA and MP. In contrast, in **Blattoneoptera + Hemineoptera + Endoneoptera**, MA is captured immediately at the basivenale by RP (or R), and is released again from RP apically after a long fusion. Thus, medial branches belong only to MP (Figs 11, 12, 17, 21B, 22B) (Kukalová-Peck, 1991, 1997; Kukalová-Peck & Brauckmann, 1992). In Dermaptera, the media is highly reduced and not informative.

Note that the fusion between MA and RP (or R) near medial basivenale (BM) as well as the separate base of MP, are almost always macroscopically obscured. This obscurity instigated decades of endless debates, erroneous homologizations, and unfounded criticism. Nevertheless, the states of MA and MP described above are very easily verified in large, freshly killed Blattodea or Megaloptera, by sectioning the veinal bases under water (K.D. Klass & JKP, personal observation).

The wings are flexed backward in the resting position in Pleconeoptera + Orthoneoptera and are wrapped around the body dorsally and laterally (especially near the

wing base). In contrast, in Blattoneoptera + Hemineoptera + Endoneoptera the wings are flexed in a roof-like position (low or high), or are dorsally flat. The position of flexed wings in Dermaptera and Dictyoptera is identical: Dorsally flat.

The internal folding of the anojugal lobe in Pleconeoptera + Orthoneoptera is regularly fan-like, with equal distances between the folds. In Blattoneoptera + Hemineoptera + Endoneoptera the folding is irregularly fanlike: Some folds may be added, and they may cross some anal veins. Dermaptera share with Dictyoptera AP1+2 bearing added secondary branches; Dermaptera also contain several added apomorphic folds (see Table 6E).

The oldest wings of Blattoneoptera are known from the Middle Upper Carboniferous (Westphalian). Some belong to the blattoid stem line (probably related to Isoptera, see Table 6F, G), and others to the living order Blattodea. Protelytroptera, the polyphyletic stem line including the direct ancestors of Dermaptera, is known from the Early Permian, but is almost certainly older than the dictyopteroid line (some dermapteroid and Dermaptera characters are more plesiomorphic than in Dictyoptera, see Table 6D–G).

Contrary to the opinion of some, the wing complex, if properly used, is actually convincingly and exceptionally richly informative at higher systematic levels. And, the fluctuation of size, amount of sclerotization, the number of small branches, on top of unpredictable variability and reversals, often makes wing characters uncertain and not very useful at the species and genus level.

With a fully homologized wing complex, the Pleconeoptera and Orthoneoptera share several synapomorphies with each other, but none with Blattoneoptera, Hemineoptera, or Endoneoptera (see Table 6B). Consequently, the taxon Polyneoptera of Martynov (1940) (plecopteroids + orthopteroids + blattoids) and its alleged stem lines (cumulatively called "Protorthoptera") are both polyphyletic and should be abandoned (Kukalová-Peck, 1991; Kukalová-Peck & Brauckmann, 1992; Kukalová-Peck & Peck, 1993).

Accurately homologized wing veins, wing lobes and wing articulation convincingly put Dermaptera into Blattoneoptera (Table 6D, E). Dermaptera share with Dictyoptera the following hindwing character states. (1) A partial anojugal lobe, (2) a shortened, shallow claval fold, (3) a well pronounced, long and deeply incised anal fold, (4) a significant narrowing of the AA field, (5) a typically blattoid (very strongly) extended AP field, and (6) the presence of secondary, serial, terminal branches on AP1+2. For additional character states see Table 6B–H

The relationship of Dermaptera within Blattoneoptera

The relationship of Dermaptera to other neopterous orders was more recently discussed by Štys & Biliński (1990), and by Kristensen (1995). Those authors concluded that, because of a similar ovarian structure, Dermaptera are a prospective sistergroup of Hemineo-

ptera + Endopterygota. This implies that Dermaptera are either not a member of the Blattoneoptera, or that Blattoneoptera are paraphyletic.

We do not share either view. The autapomorphies of the Blattoneoptera, occurring in the Grylloblattodea (Notoptera), Dermaptera, and in Dictyoptera, are as follows. The pronotum is disc-like and flat. The flexed wings lie horizontally on the abdomen and they are articulated far forward at the anteriormost corners of the metanotum. The postnota are reduced. The flight motor system is highly modified in the same, complex way (Boudreaux, 1979, his Fig. 71, p. 207; CSIRO, 1991, p. 320; Brodsky, 1994). Another alleged autapomorphy of the Blattoneoptera, the strongly slanted pleural suture (Boudreaux, 1979), appears to be a later development because it is not visible in *Acosmelytron delicatum* (Fig. 18).

All members of Blattoneoptera (except the predaceous Mantodea) live on the ground, in litter, crevices or other hidden places. It seems that running away from predators and hiding in narrow places, rather than flying away, was the main survival strategy of ancestral Blattoneoptera. Grylloblattodea, Dermaptera and Dictyoptera show very distinctive adaptations for hiding, such as the dorsoventrally flattened body (Blattodea), accompanied by laterally overlapping abdominal tergites and sternites (Dermaptera), the strongly slanted pleura (Grylloblattodea, Dermaptera, Dictyoptera), and the large coxae with strong muscles for running (Grylloblattodea and Dictyoptera) (Boudreaux, 1974; this paper).

In the wing structure, **Dermaptera and Dictyoptera** share important blattoneopteran characters, which are clearly recognisable, even if sometimes differently modified (Table 6E). The blunt ridge replacing ScA in Dictyoptera is also present in Dermaptera, but is changed into an overhang. The radial basivenale (BR) is also long and swollen, but variously shaped. The medial basivenale is also right-triangular, enlarged and separated from BR by a conspicuous furrow, but its proximal margin is membranized. The 2Ax body (AXM) is also wrinkled and bears an arched proximal margin, but it is narrower and more twisted. The 3Ax anal arm (FA) is also very prominent, but differently shaped and extended by incorporating FJ. The posterior wing process (PWP) is also desclerotized, but much narrower. The wing attachment is also broader than the wing articulation. These wing character states are absent in the ground patterns of Orthoneoptera, Pleconeoptera, Hemineoptera, and Endoneoptera (Figs 14–17, Table 6B–H).

The presence of several "dictyopteroid" character states in the fossil stem line of Dermaptera, such as tarsi with five tarsomeres and annulated cerci, clearly shows that the tarsi with three tarsomeres and forceps-like cerci in extant Dermaptera are not part of the ancestral dermapteran ground pattern and evolved later.

The relationships of extinct "Archidermaptera"

The results obtained in this study partly confirm and partly reject the previous hypotheses on the relationships of fossil Dermaptera. The "Archidermaptera" are clearly a

paraphyletic assemblage of those fossil species that cannot be referred to extant families, as was also concluded by Willmann (1990). Their status as a separate "suborder" (Carpenter, 1992; Sakai, 1996; and others) is not supported by any autapomorphy and should be abandoned.

Vishnyakova (1980) used the "phenetic-similarity" approach to "archidermapteran" relationships. In spite of this different method, the results are to some extent similar to ours. Vishnyakova proposed a close relationship between *Dermapteron* and *Turanovia* and grouped them into one subfamily. The sistergroup relationship between the genus *Dermapteron* and *Turanovia* is also supported here (character 54), but analysing the genus level is beyond the scope of this contribution. According to Vishnyakova (1980), the genera *Archidermapteron, Asiodiplatys, Microdiplatys* and *Protodiplatys* belong to the Protodiplatinae. They indeed appear also to be monophyletic in our analysis.

The results presented here contradict Vishnyakova (1980) in that the genera *Semenoviola, Semenovioloides* and *Turanoderma* are members of the extant "Pygidicranidae". Extant Dermaptera share as derived characters the reduction of ocelli and the special structure of the female abdomen. In contrast, the fossil genera show the plesiomorphic states of these characters. It is quite possible that *Archaeosoma martynovi* and the genera mentioned above represent the sistergroup of extant Dermaptera.

Extant Dermaptera, in spite of being quite markedly different from the rest of extant insect taxa, share only two ambiguous apomorphies: The reduction of ocelli, and the covered 8th and 9th abdominal tergites in females (characters 44*, 52*). All other "typical" dermapteran characters, such as the loss of cercal annulation, overlapping tergites and sternites, and highly specialized wing folding, are already present in Palaeozoic and Mesozoic fossils. Thus, Jurassic fossils are easily recognized as Dermaptera (Vishnyakova, 1980) even if the wing venation and articulation is not visible. In extant Dermaptera, there is remarkably little morphological and ecological variation. A similar close adherence to an ancient ground pattern can be observed in Blattodea.

The evolution of characters is not presented in detail, because of the great number of equally parsimonious trees. However, some aspects in evolution of the characteristic wing folding are discussed below.

The relationships of extant Dermaptera "families"

Extant Dermaptera clearly constitute a monophyletic taxon, as suggested by a highly autapomorphic wing articulation, venation, and folding pattern. However, these characters are not applicable to the large number of wingless earwig species, and to the Hemimerina (African, epizootic on giant rats; Rehn & Rehn, 1935) and Arixeniina (Malaysian, epizootic on bats; Jordan, 1909). Their inclusion into the Dermaptera is justified by the possession of smooth, not annulated adult cerci (character 38), holocentric chromosomes (White, 1971, 1972) and by the most striking dermapteran body character, the lateral overlapping of abdominal tergites and sternites (charac-

ters 40, 51). Their tarsi have only three tarsomeres (characters 34, 48). None of the living, closely related groups, such as Blattodea share these derived character states.

Hemimerina and Arixeniina are most often considered as "suborders" of the Dermaptera, because they are conspicuously different in many features. However, both taxa have acquired a high number of autapomorphic characters due to their peculiar life styles, as is common in epizootic or parasitic taxa. These autapomorphies obscure the characters showing the relationships with existing dermapteran taxa. We assume that Arixeniina and Hemimerina are indeed the sistergroup or a subtaxon of a dermapteran "family", as was proposed by Popham (1985) for Arixeniina (called Arixeniidae) and recently by Klass (2001). The latter author found detailed similarities in the abdomen of *Hemimerus* and other forficuline taxa.

Because the new characters presented here are concerned with the wing venation and articulation, the systematic position of the Arixeniina and Hemimerina is not discussed in this account.

The above results partly confirm and partly contradict the findings of Haas (1995). The exclusion of the Karschiellidae and "Diplatyidae" from the "Pygidicranidae" is confirmed, as is the paraphyly of the "Diplatyidae". The monophyletic state of the "Pygidicranidae" has been doubted by Haas (1995) on grounds of the four virgae in Esphalmeninae and Pyragrinae. The results here support this view because the reduced number of virgae (to two) is shared by all species of *Echinosoma, Tagalina burri*, and *Allostethus indicum*, by Apachyidae, Anisolabididae, "Labiduridae", and by Eudermaptera (character 42). In contrast, the last common ancestor of extant Dermaptera probably had two unidirected genital lobes with four virgae. Later, the two genital lobes became bidirected (character 41) and finally one genital lobe was reduced. The latter apomorphic condition is found in the Eudermaptera (Forficulidae + Spongiphoridae + Chelisochidae).

The present results contradict the view of Popham (1985) on the evolution of male genitalia. Popham considered the "Pygidicranidae" to be monophyletic because of the structure of the male genitalia, interpreted here as plesiomorphic. Popham further assumed that the reduction of one genital lobe occurred twice, in Spongiphoridae and again in Chelisochidae + Forficulidae. We assume that it occurred only once.

In the present contribution, Apachyidae and Anisolabididae appear to be monophyletic families. This result is not definitive, because only one winged species of each taxon was available to us for study. Most species of the Anisolabididae are wingless and their classification is largely based on body characters. Their sistergroup relationship with the Eudermaptera (Haas, 1995) is not supported here, because the assumed shared derived characters (characters 29–31; or, characters 5–7 of Haas, 1995), were found here to be erroneously coded.

The monophyly of the "Labiduridae" (excluding *Allostethus indicum*) is not unambiguously supported because they seem to constitute an assemblage of superficially similar Dermaptera. This notion is further strength-

ened by the taxonomic history of the "Labiduridae". According to Burr (1911), "Labiduridae" contain all Protodermaptera except the "Pygidicranidae", namely: Esphalmeninae, Psalinae, Labidurinae, Parisolabinae, Brachylabinae, Platylabinae and Allosthetinae. Later on, more and more groups were removed from this taxon. For example, the Esphalmeninae are now recognized as "Pygidicranidae" (Steinmann, 1986). Some authors, like Brindle (1965b), included the Apachyidae into the "Labiduridae". In contrast to "Labiduridae", Apachyidae and Forficulidae are taxonomically almost unchanged since their study by Burr (1911), suggesting a much more distinctive character set than in "Labiduridae".

For the first time, the sistergroup relationship of the "Labiduridae" to the Eudermaptera is suggested (characters 5, 6*, 8*, 11, * ambiguous character). Popham (1985) took the view that "Labiduridae" are the sistergroup of Forficulidae + Chelisochidae, based on an elongated second tarsomere and the presence of the basal vesicle (characters 35, 43). As pointed out earlier (Haas, 1995), the elongation of the second tarsomere is very variable in the "Labiduridae". So it was not possible, in contrast to Popham (1985), to establish a clear distinction between the "Labiduridae" + Forficulidae + Spongiphoridae and the other dermapteran "families". According to the hypothesis presented here, the presence of a basal vesicle (character 43(1)) is an apomorphy shared by *Allostethus indicum*, Apachyidae, Anisolabididae, "Labiduridae" and Eudermaptera, with two independent secondary reductions, in the Anisolabididae and Spongiphoridae. However, the sistergroup relationship of "Labiduridae" and Eudermaptera might explain the similarities noticed by Popham (1985).

In contrast with Popham (1985), the Eudermaptera are considered here to be monophyletic. There are 14 characters from different body regions supporting the monophyly. In fact, Eudermaptera (Forficulidae + Spongiphoridae + Chelisochidae) are better supported than any other dermapteran taxon discussed in this account.

In the present contribution, the sistergroup relationship between the Chelisochidae and Spongiphoridae is suggested (characters 5, 8*, 10). Previously, Zacher (1912) grouped Chelisochidae and Spongiphoridae under the "Labiales", but this proposition was not followed by later authors. Haas (1995) considered Forficulidae and Chelisochidae to be sistergroups, but this relationship is not supported by new evidence.

The above results show that most Dermaptera "families" are either not monophyletic, or only one autapomorphy is known. Future research should focus on this problem and on the autapomorphic characters states for all genera and families, which need to be identified. This task is especially urgent in the species-rich families Anisolabididae and Spongiphoridae. An improved understanding of their phylogeny will considerably improve insight into the evolution of Dermaptera.

Are the Zoraptera member of the Blattoneoptera?

The position of Zoraptera remains uncertain. The Zoraptera are hemimetabolous, which rules out a close relationship with the Endoneoptera. They have a generalized head, chewing mouthparts, and lack the enlarged cibarial sucking pump, domed clypeus or any other hemineopteran mouthpart adaptations. This rules out a close relationship with the Hemineoptera. So, the Zoraptera remained plesiomorphic regarding to development and mouth parts. However, they bear a reduced postnotum of the blattoid type, large cylindrical blattoid coxae, and the highly derived flight motor as in Dictyoptera (consisting of wing attachments shifted to the utmost-anterior corners of thoracic terga); reduced phragmata; and highly reduced indirect flight musculature (Boudreaux, 1979, p. 215; Rasnitsyn, 1998). The male genitalia appear to be blattoid (Smithers, 1991). The wing venation is compatible with blattoids but the decisive wingbase characters are destroyed by petiolation (Kukalová-Peck & Peck, 1993). A membranized posterior wing process (PWP), if present, should provide a convincingly blattoid character, but it has not yet been available for observation.

The "non-blattoid" characters of Zoraptera include tarsi with only two segments, cerci that lost their annulation, and a pronotum that is not disc-like. But these characters may easily be apomorphies due to the small body size and a special life cycle. The thoracic pleural sulci are not slanted, but neither were those in the dermapteran ancestor *Acosmelytron delicatum* (Fig. 18).

Rasnitsyn (1998) rejected the association of Zoraptera with Blattoneoptera: Dictyoptera for two reasons. (1) Zoraptera bear on the pterothorax an invaginated sternum forming an internal ridge, which also occurs in Hemineoptera and Endoneoptera but not in Blattoneoptera. But this inner ridge is not a convincing character because it occurs convergently in groups with very broad coxae and narrow sternum, such as in unrelated damselfly-like extinct Megasecoptera (Palaeoptera) (personal observation by JKP). Recently, Rasnitsyn & Novokshonov (1997) removed Hemineoptera from Neoptera and combined them with extinct Palaeodictyopteroidea under Palaeoptera. This assumption breaks the convincingly monophyletic Neoptera ground pattern (see massive evidence supporting Neoptera monophyly in Table 6A), and also contradicts Rasnitsyn's (1998) interpretation of the internal sternal ridge as a possible synapomorphy for Zoraptera, Hemineoptera and Endoneoptera. (2) The identical wing motor system in Dictyoptera and Zoraptera is rejected as a possible synapomorphy because Rasnitsyn found reduced indirect flight musculature both in Zoraptera and in Xyelidae (Hymenoptera). But the muscle reduction and the Dictyoptera motor system are two different character sets. The muscle reduction in Zoraptera is part of a coevolved, integrated flight motor system, which also occurs in Dictyoptera (Boudreaux, 1979; see description above). In contrast, the muscle reduction in Xyelidae is limited to this family. Endoneoptera including Hymenoptera share the plesiomorphic neopterous flight

motor system (Brodsky, 1994). Therefore, the reduction of indirect flight muscules in Xyelidae is not part of the identical and complex flight motor system as in Zoraptera and in Dictyoptera, but an unrelated homoplasy.

Rasnitsyn (1998) proposed that Zoraptera belong to the extinct Palaeozoic "superorder" Caloneurodea, believed by him to be the sistergroup of Endoneoptera. But, Caloneurodea bear a typical, hemipteroid, domed clypeus above the cibarial sucking pump and typical stylet-like mouthparts (*Paleuthygramma tenuis*: Kukalová-Peck, 1991: Fig. 6.22; note that the last character is mentioned also by Rasnitsyn, 1998). Head characters and venational systems identify the extinct Caloneurodea as ancestral hemipteroids (Kukalová-Peck & Brauckmann, 1992). In contrast, head morphology shows that Zoraptera are neither hemipteroids, nor a member of Caloneurodea. Referring the controversial modern insect order to an extinct, poorly known taxon is extremely risky (Hennig, 1969, 1981).

The above review of Zoraptera characters indicates that the relationship with Blattoneoptera: Dictyoptera is, under the circumstances, the most parsimonious choice. But the evidence seems insufficient for a definitive decision. For that reason, we choose not to include Zoraptera in the cladistic analysis.

FUNCTION AND EVOLUTION OF THE DERMAPTERAN HINDWING

The hindwings of Dermaptera are highly derived in several aspects of their venation pattern. They are the only wings known to us, in which veins do not radiate from the articulation, but from a region almost in the centre of the wings (Fig. 2). Each radiating and intercalary anojugal branch contains a broadening where it is dissected by the ring fold. The broadenings, which look like "weakened" joints, actually provide strong veinal support for the fan. In comparison with Coleoptera, which also bear transversely and longitudinally folded hindwings (Haas, 1999; Haas et al., 2000), the dermapteran hindwings have a very broad attachment to the metanotum, which is much broader than the area occupied by the articulation. Also, the hindwing base is exceptional in containing special bending zones, and a large central membranized area. All these morphological peculiarities accompany and make possible the special folding pattern and folding mechanism, described below.

Dermaptera wing folding mechanism

Dermaptera hindwings are unique within the Pterygota in being able to fold an enormous anojugal lobe, which is almost 10 times larger than the squama (Haas, 1994). This is achieved by folding the wing four times, as shown in Fig. 2. (1) By a fan-wise folding of the anojugal lobe along the radiating folds. (2) By a transverse fold between the squama and ulnar area on one side, and the inner and outer apical area, and the bases of the radiating branches on the other side. (3) By a bending of the radiating and intercalary branches along the ring fold. (4) By the longitudinal folding along the border of the squama to the ulnar area. The dermapteran folded wing forms a wing

package with the squama as the dorsal surface, and the ulnar area as the ventral surface. The anojugal lobe is densely folded between the squama and ulnar area. The four steps of folding actually take place almost simultaneously and they are dependent one on another, so that they are not clearly separable. The reader is encouraged to photocopy and enlarge Fig. 2 and to fold it into a paper model of an earwig hindwing. When properly manipulated, this model will fold and unfold, and show the folding mechanism.

This complex folding is achieved entirely by intrinsic elasticity in the wing, because the wing continues folding automatically in freshly killed specimens. The forces are mainly generated by the broadenings in radiating and intercalary branches (Kleinow, 1966; Haas et al., 2000). In contrast to their morphological appearance, the broadenings are not weakened portions in veins, but are active force-generating centres. They are the key element for folding the large fan. By bending the veins along the ring fold, the whole fan starts closing, as in the model. Finally, the ulnar area is tucked under the squama by the elasticity in the longitudinal fold (Kleinow, 1966; Haas et al., 2000).

The broad attachment of the wing to the thorax is of major functional importance. As long as the attachment is undamaged, the wing package pulls itself automatically towards the thorax, as a result of forces generated along the longitudinal fold. If the wing attachment is partly destroyed, so that the attachment is limited to the articulation, the wing does not return to its resting position (Haas, 1994; Haas et al., 2000). The elasticity in the longitudinal fold pulls the anojugal fan, which is attached to the metanotum, into the wing package; this returns the wing to its final resting position (Kleinow, 1966; Haas et al., 2000).

Since intrinsic elasticity folds the wing, a different mechanism must be employed to unfold it (elasticity cannot be effective in opposite directions). To unfold the wing, the wing package is erected over the thorax (Kleinow, 1966; Haas et al., 2000). This movement will automatically open the wing package: The anojugal fan is pulled out by its attachment to the thorax, the wing package is opened, and the squama and ulnar area assumes an angle of about 90°. Next, the abdomen bends over, and the cerci interact with the wing package and unfold ("unzip") the wings. Both wings are simultaneously erected, but they are unfolded one after the other (Kleinow, 1966; Haas et al., 2000).

Because the wing automatically folds by its intrinsic elasticity, counter-acting structures and mechanisms are needed to keep the wing unfolded. The stiffening is achieved by two mechanisms: The central wing hinge (*Flügelmittelgelenk*), and the concave longitudinal fold (clf) (*konkave Längsfalte*, both terms of Kleinow, 1966). The central wing hinge consists of four plates: Squama, ulnar area, outer apical area, and inner apical area. These plates are arranged so that the angles around their centre do not add up to 360°. Therefore, this bi-stable mecha-

(A)

(B)
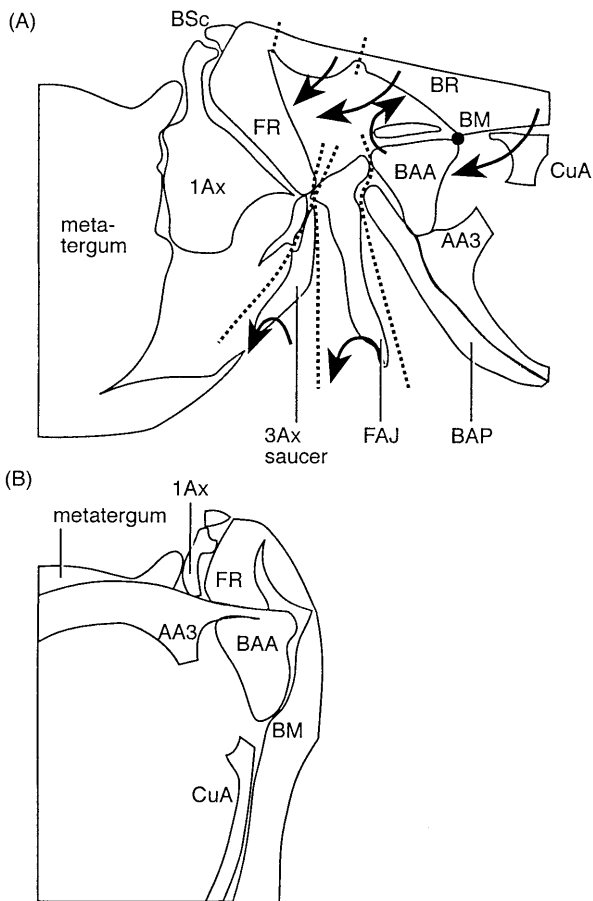
Fig. 25. Movements of the hindwing articulation sclerites during folding. Arrows indicate the movement of single sclerites, while thick lines indicate the turning or pivoting axes. Scheme based on observation of *Labidura riparia*.
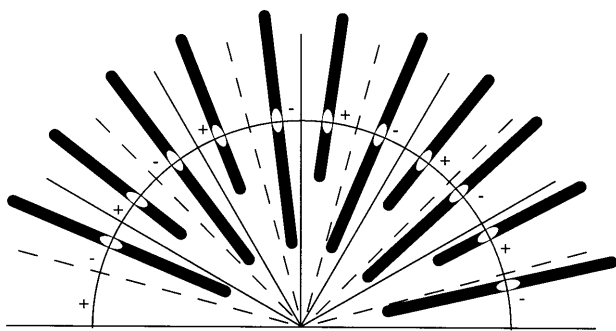
Fig. 28. Photocopy and enlarge this figure twice and fold it according to the following instructions. Fold one model so that the solid straight lines are convex and the dashed lines are concave. Now bend the fan beyond the circle to the left, so that the convex/concave relation of the circle line results. Fold the second model so that the dashed lines are convex and the straight solid lines are concave. In this second case, the part beyond the folding line has to be bent to the right in order to produce the convex/concave relation of the circle line. These models demonstrate that the bending direction of the part beyond the circle line can be changed without changing the bending directions of individual veins.
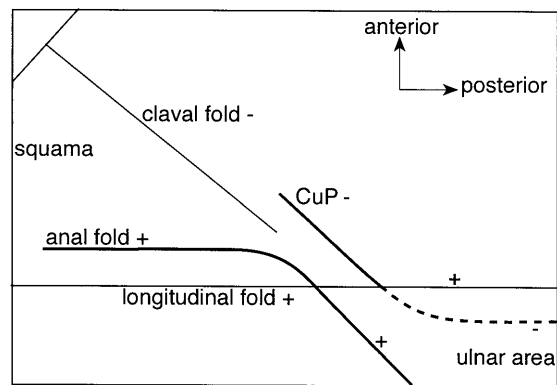
Fig. 26. Model for the wing stiffening mechanism composed of the claval and anal fold, squama and ulnar area, and CuP. The reader is encouraged to photocopy and enlarge the figure and fold it according to instructions. For further explanations see text.

nism is used to stiffen the wing (Haas & Wootton, 1996; Haas et al., 2000).

The second essential stiffening mechanism is the concave longitudinal fold (clf). The wing is kept unfolded by counteracting the elastic forces along the longitudinal fold (lf) (Kleinow, 1966). The clf is snapped through during the wing unfolding by the cerci, and probably released by the action of the wing articulation; we assume it is a movement of 3Ax. A paper model demonstrates quite well the function of the clf. The reader is encouraged to fold a sheet of paper longitudinally, so that a convex crease (i.e., the lf) appears, and afterwards obliquely, so that a concave crease (i.e., the clf) intersects the first crease at an angle. As long as the oblique, concave crease is not snapped through, the two halves, separated by the convex crease, are freely movable. The sheet becomes locked if the concave crease is snapped through.

Kleinow (1966) believed that the concave longitudinal fold (clf) is only one fold. Our research shows that it actu-
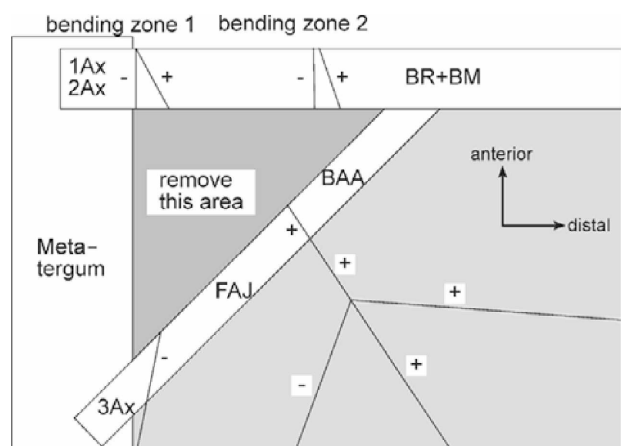
Fig. 27. Model of the dermapteran wing articulation, to explain the straightening of the bending zones in the anterior wing margin, and the probable release mechanism of the stiffened wing. The reader is encouraged to photocopy and enlarge the figure and fold it according to instructions. For further explanations see text.

ally consists of two, and sometimes three, folds: A short claval fold between CuP and AA3, a somewhat longer anal fold just in front of AP, and a broad, flat CuP remnant, sometimes expressed as a concave fold. The claval fold is concave when active, and it begins close to the tip of BA. It never crosses, though it often comes close to, the longitudinal fold (lf) between the squama and ulnar area. The anal fold is convex and it runs close to AP. The part of the anal fold involved in the stiffening of the wing begins without a definitive origin near the base of AP. It extends distally, crosses AP, and joins the transverse fold.

Although the morphological interpretation of the folds is different from that described by Kleinow (1966), his functional considerations are correct. It is the crossing of a convex fold by a concave fold, which keeps the hindwing unfolded along the border of the squama and ulnar area. However, this is achieved by a combination of several folds, and not by a single fold. The (concave) claval fold ends just in front of the (convex) longitudinal fold, but yields a second fold as a continuation (Fig. 26). If the claval fold would cross the folding line between the squama and ulnar area, veins CuP and AA would have to be flexible at this line, but flexibility is probably not reconcilable with their stiffening function.

In some species of Dermaptera, especially in the more sclerotized ones, a third concave fold is found. It sometimes begins as a continuation of the claval fold, and sometimes just anterior to it, probably as a small remnant of CuP. It ends by fading in the ulnar area between CuA3+4 and AP. No experiments were done with living specimens, but the presumed function of this fold is to provide an additional folding line, strengthening the concave longitudinal fold (clf). Clf is now a strip of sclerotized wing membrane, which crosses the longitudinal fold and stiffens the wing by its almost vertical position (Fig. 26). This induces a stronger corrugation, necessary to counteract the folding forces in the longitudinal fold.

Wing articulation and folding

The dermapteran hindwing articulation contains many unique characters. Compared with Dictyoptera (Figs 11–13), the dermapteran median plate is desclerotized and replaced by a large membranous area (Brodsky, 1994) (Figs 7–10; median plate, i.e. medial and cubital fulcalare, FMCu). Note that a weakly preserved median plate is still retained in *Pyragra fuscata* (Fig. 7B). The part of the medial basivenale BM adjacent to the median plate is also desclerotized. The combined radio-medial basivenale BR + BM is enlarged and has two bending zones. Axillary sclerite 1Ax is large compared to Blattodea and Mantodea (Brodsky, 1994) (Figs 7A, 11, 12). All these deviations from the Blattoneoptera ground pattern are due to the movements of articular sclerites during wing folding.

The large membranous area in the centre of the articulation, previously occupied by the median plate, is where several folds intersect (Fig. 25A). It is crumpled in the folded wing, but outstretched in the unfolded wing. One fold originates in each of the two bending zones of BR + BM; three other folds begin close to the FAJ and project

into this area; another fold starts between BAA and BM (Fig. 25A). This arrangement of folds is only possible in a soft, pliable membrane; stiff material, such as paper, is not flexible enough. Therefore, it is impossible to build an accurate paper model with all folds present in this area (Fig. 27). The specific arrangement of folds reflects the movements of the articular sclerites during folding. The function of the membranous area is to allow crumpling, and to provide space into which BAA and the anterior part of FAJ are turned. During wing folding, combined basivenale BR + BM is flexed in two bending zones. BAA turns about its pivot with the BM, which makes the proximal corner of BAA draw near BR. FAJ is turned upside down and it lies underneath AA3 + BAP in the folded wing (Figs 25, 27).

The presence of two bending zones (proximal and distal) in the combined basivenalia BM + BR is surprising, because dermapteran basivenalia are loaded during flight and any bending seems counterproductive. However, Kleinow (1966) noticed the straightening of the proximal bending zone. This is achieved through lowering the metanotum by a contraction of tergo-sternal muscles. This pulls the median margin of 1Ax ventrally, and pushes its lateral margin dorsally. This tilt promotes the wing, erects the wing package over the body, and simultaneously straightens the proximal bending zone in BR + BM. But, the distal bending zone is unaffected by this movement. We assume, based on observations by Kleinow (1966) and the model (Fig. 27), that the distal bending zone is also straightened (but indirectly) by the cerci.

As described above, the abdomen bends over, the cerci interact with the wing package, and they unfold ("unzip") the wing. This action simultaneously stretches the membrane of the articulation, and the sclerites are passively pulled apart and into their flight position. The 3Ax, FAJ and BAA are expanded to form a rod in the flight-ready wing. As inferred from our own observations on *Labidura riparia,* the paper model, and Kleinow's data, the rod keeps the metanotum and BM at a distance and the bending zones in BR + BMA straight (Fig. 27). This action prevents the wing from folding automatically. The arrangement is apparently stable enough to allow the movements of the wing base during flight, and to withstand the aerodynamic forces. After landing, the rod is unlocked by turning 3Ax about its long axis, which is the usual way of folding wings in the Neoptera (Snodgrass 1935).

The differences between the wing articulation of Blattodea and Dermaptera mostly reflect the differences in wing folding mechanisms. In Blattodea, the hindwings are unfolded simply by promoting them, even if their apical part is transversely folded (Haas & Wootton, 1996; Haas, 1998). In Dermaptera, the wing is unfolded by the cerci (Kleinow, 1966; our own observation), which eliminates the need for a mechanical system of unfolding the wing from its base. The use of cerci also provides freedom for further transformations in folding pattern and mechanism. By using the cerci to unfold their wings, Der-

maptera evolved a folding pattern, which is far too complex to be unfolded from the wing base.

Wing venation and the evolution of folding

The wing folding and venation patterns in extant Dermaptera are almost perfectly uniform (Haas, 1995). The complexity of these patterns suggests that they evolved only once. The fossil record of the Dermaptera and their stem line, the "Protelytroptera", gives some clues to the evolution of folding and venation patterns, even if most fossils do not have unfolded wings (Carpenter, 1933, 1939; Carpenter & Kukalová, 1964; Kukalová, 1964b, 1966, 1969). The only known exception is dermapteran stem line representative *Protelytron permianum*, with hindwings showing a relatively simple folding pattern.

The comparison of folding patterns in Dermaptera and *Protelytron permianum* (Figs 2, 19) shows that the former is folded twice transversely, whereas the latter has only one transverse fold. The transformation could have happened in the following way.

The hindwing of *Protelytron permianum* has four principal folding lines. (1) The anal fold, which is the fold running between AA4 and AP, and between RP+MA and AP (this folding line is not indicated by Tillyard (1931) but is necessary to fold the fan under the remigium). (2) The folding line termed "nf" (or ring fold) running from the posterior wing margin to point "k". At the intersection of nf and the radiating branches, broadenings termed "chitinous patches" are shown (Tillyard, 1931). (3) The folding line running from point "k" to the anterior wing margin, and reaching it at point "n". The latter two folds (nf and fold from point k to n) are certainly new in Pterygota; they allow the wing to fold ventrally - transversely.

And finally (4) the folds located between the radiating branches of AP (all dotted lines in Fig. 19).

Later in evolution, the fold "nf" shifted distally, accompanied by a change in shape and relative proportions of wing areas, and reached the anterior wing margin independently from the fold "k-n". Consequently, the anal fold was retained in functional relation with the "k-n" fold, but lost its connection to "nf" fold.

Simultaneously, fold "nf" had to change from convex to concave. This step might seem improbable but for the complex function of the broadenings in extant Dermaptera (Kleinow, 1966; Haas et al., 2000). There, forces are generated which bend the radiating branches dorsally along the ring fold and the intercalary branches ventrally. Considering the specialized structure of the broadenings, a reversal of the bending direction would imply major changes in these structures. However, these are not necessary when the convex-concave pattern of the radiating folds is reversed. Then, the bending direction of the transverse fold can change without changing the bending direction of the broadenings (Fig. 28).

In addition to this folding, the dermapteran hindwing also folds longitudinally. Simple geometric reasoning shows that the longitudinal fold evolved after the transverse folding, which is also suggested by the fossil *Protelytron permianum*. A sheet of paper will clarify this immediately: First, fold the sheet longitudinally and then,

transversely. After unfolding the paper, the longitudinal fold will be convex throughout its length, whereas the transverse fold changes from convex to concave at the intersection point with the transverse folding line. Folding the paper first transversely and then longitudinally results in a reverse situation, when the transverse fold is convex throughout, and the longitudinal fold changes from convex to concave.

Exactly the same succession as in the paper folds above occurs in the dermapteran wing in the central wing hinge (*Flügelmittelgelenk* of Kleinow, 1966), where the inner and outer apical areas, squama and ulnar area meet. Here, the longitudinal fold changes its orientation from proximally convex to distally concave, but the transverse fold remains convex. The same configuration of folds confirms that the anojugal lobe has been folded fan-wise before being folded transversely. However, it is not possible to deduce whether the folding line "nf" moved distally before or after the longitudinal fold evolved, because the intersection area is reduced. It should also be noted that the new longitudinal fold is running across both the remigium and the anojugal lobe.

The fossil "Archidermaptera" give no information about the evolution of hindwing folding in the Dermaptera. The oldest known Dermaptera are Jurassic in age (Vishnyakova, 1980) and already had a small wing package. The hindwings were probably already folded by the autapomorphic dermapteran folding pattern and folding mechanism. Because Jurassic Dermaptera possessed long, annulated cerci, and a small wing package, the cerci were probably used to unfold the hindwings the same way as in extant Dermaptera (for other cercal functions in extant Dermaptera see Briceño & Eberhard, 1995). Consequently, short and smooth cerci are not an adaptation to hindwing unfolding. Incidentally, all known "Protelytroptera" with no or simple hindwing folding bear short cerci.

HIGHER TAXA AND SPECIES REQUIRE DIFFERENT METHODOLOGIES IN CHARACTER ASSESSMENT

Phylogenetically informative morphological characters of insect species are selected and assessed by direct observation and comparison. They are usually (1) not very difficult to recognize, (2) numerous, and (3) not very difficult to homologize. The major drawback is that they are (4) frequently unstable and open to unrecognizable reversals. Phylogenetic methods using parsimony and consensus are designed to deal with back mutations and other complicating factors.

In contrast, phylogenetically informative, stabilized characters in higher taxa of insects are exclusively only those embedded in their ground patterns. The characters are invariably extremely old (minimum 100–350 my; Marshall et al., 1994; Raff, 1996). The problems with higher taxa are very different from those encountered in species. (1) Ground pattern characters are relatively few. Therefore, each error potentially has a large impact. (2) They are sometimes difficult to find in extant insects because they have been hidden under later (suborder-through-species level) reductions, fusions and extensions.

(3) They must be very carefully and fully homologized, because the putative "homologue" is too often a homoplasy. But, full homologization must include the related orders and superorders, a very broad and sometimes unmanageable task. (4) The modes of character transformation are actually very few (reductions, fusions, braces and extensions) but they occur in parallel at very many unrelated taxonomic levels. The paucity of choices versus frequent co-occurrences creates a huge web of homoplasies. (5) The unrelated complexes are frequently adapted to a similar function. This also generates homoplasies. (6) Most of the higher-level characters are integrated in old morphological complexes (wing complex, mouthparts, pleura, genitalia, terminalia, etc.), which generate function by working together, and which are readily identifiable only as a complex. Such characters neither function nor evolve individually. Handling them as if they *were* independently functioning and evolving, means imposing on nature a process that does not exist. Not surprisingly, it is only *after* a character complex is disassembled and its characters are evaluated at too high a level (e.g., under Pterygota instead under Blattodea) that higher character states turn homoplastic. Note that the same observation is valid also for the limb-derived arthropod appendages on the head (e.g., the much disputed "synapomorphic" mandible in Odonatoptera and Neoptera), the thorax, and the abdomen.

Assessing order-level characters outside their orders always creates homoplasies. As a pertinent example, the stem of M (= a derived fusion of MA + MP) is an apomorphy. M occurs in the representatives of Pleconeoptera, Orthoneoptera, Ephemeroptera and Odonata. Under *Pterygota*, M shows these groups as related, which is a homoplasy unsupported by other wing characters. In contrast, under Palaeoptera M supports palaeopterous monophyly (all Palaeoptera share the stem of M and the stem of Cu; these two stems are absent from the ground pattern of Neoptera). This monophyly and sistergroup relationship is supported here in Table 6A by 63 additional characters. Under Neoptera, the rise of M supports the basal division of Neoptera into two groups: Pleconeoptera + Orthoneoptera (M is formed and shared) and Blattoneoptera + Hemineoptera + Endoneoptera (M did not form). This division is supported in Table 6B by 28 additional characters.

Most important, no character complex will yield good results in character analysis if some characters are left out. As an example, the previously overlooked vein ScA+ turned out to be very important in analyzing Orthoneoptera, Blattoneoptera and Endoneoptera. The equally overlooked precostal strip (PC) polarizes Palaeoptera and Neoptera, defines orders in Hemineoptera and superfamilies in Coleoptera (Table 6A, H). The precise nomenclature of anal veins, which were previously randomly serially numbered as 1A, 2A, 3A, provides documentation that Neoptera contain two groups of superorders with differently composed anojugal lobes (Fig. 22). The wing function (wing folding, flight flexion lines), previously seen as separate topic, became very important in

revealing higher- level homoplasies and transformations, etc.

The coding of wing characters in the ground patterns of higher taxa is a quite different process than in species. Importantly, coding is by no means intuitive. Neither does it use the ancestral or democratic method (sensu Prendini, 2001). Instead, it observes evolutionary steps, in which the character complexes evolved. Principal wing veins and articular sclerites evolved from being present, to becoming gradually reduced and then lost; and, from being independent (separate), to becoming braced and then progressively fused. A principal vein or articular sclerite in a ground pattern when fused, does never unfuse and when completely reduced and lost, does not reappear. There are no reversals in the higher ground pattern characters in any representatives (see Table 6). This observation so far has never been falsified. Thus, the character coding in Table 6 is based on the predictability of evolutionary changes in the descendants. We know that sister-groups share similar fusions, extensions, reductions and losses. We also know that each next step in wing evolution will bring further fusions, reductions and losses in the descendants. If fusions and losses are "removed" from a ground pattern, the ancestral condition is revealed. If we continue long enough in "removing" derived characters, we reach the hypothetical protowing, without braces, reductions or fusions.

The phylogenetic tree lends itself to reconstruction only because the ground patterns of higher taxa are composed of stabilized character states (i.e., expressed in all representatives and without any reversals). If they were not stabilized, any higher taxon would sooner or later dissipate and could not be described or visually recognized in living species. Only the stability of ground pattern characters over hundreds of millions of years makes it possible to have higher taxa and to arrange them into phylogenetic trees.

Thus, higher phylogenetics is completely impracticable without first finding the ground pattern character states in all potentially related higher taxa. This is achieved by visually recognizing, in each taxon, the character states shared by all its representatives. If a character is highly specialized and transformed, this transformation must be smoothly derivable from the shared ground pattern state. This search is obviously a long-term undertaking.

In summary, the only phylogenetically informative morphological character states in the higher taxa are those contained in their ground pattern. The ground pattern characters must be carefully identified, fully homologized, and none must be left out. They must be judged at all times within a double context: (1) of the own morphological character complex and its function, and (2) of the ground pattern of the indigenous taxon. In the neopterous and palaeopterous higher taxa, the fusions, reductions, braces and extensions are added step-wise. They define the superordinal lines, superorders, orders, suborders and sometimes families, and reflect their relationship. The process of tracing all steps (nodal transformations) is shown here only in Dermaptera. Further

information is available in the files of JKP and will be published in monographs. Note that below the family level a parsimony analysis usually brings better results than the method described above.

CONCLUSION

The relationship of Dermaptera to the other pterygote orders, as analyzed in this account and presented in Table 6, offers the following results.

Neoptera: [Pleconeoptera + Orthoneoptera] + [Blattoneoptera + (Hemineoptera + Endoneoptera)].

Blattoneoptera: (Grylloblattodea + (Dermaptera + Dictyoptera)).

Dictyoptera: (Mantodea + (Blattodea + Isoptera)).

Dermaptera: Karschiellidae + ("Diplatyidae" + ("Pygidicranidae" + (*Allostethus indicum* + (Anisolabididae + ("Labiduridae" + [Forficulidae + (Chelisochidae + Spongiphoridae)])))))). Taxa in quotation marks are probably not monophyletic.

The step-wise assembly of the dermapteran hindwing venation and articulation is much easier to understand if we offer the broad overview of nodal evolutionary changes in the Pterygota. Only a character table of the entire pterygote wing complex provides, in Dermaptera, the necessary amount of order-level information, which separates synapomorphies from overwhelming, omnipres-

ent, and otherwise "unrecognizable" homoplasies. As another advantage, a table renders the wing characters more user-friendly for study than mere description.

Constructing a complete and flawless character table of the pterygote wing complex at the higher level will probably take another decade. Nevertheless, we propose that starting the conceptualization now will contribute to the clarity of this paper, open the topic to contributions, and make easier any future use of the wing structure in higher phylogenetics. For these reasons, we offer below the first version of the fully homologized pterygote wing character table.

Table 6. The character table of the pterygote wing complex.

Introduction. The character table of the fully homologized pterygote wing complex (with emphasis on the Neoptera) is based on a long-term study of the wing complex (wing venation and articulation) by Kukalová-Peck. Symbols for veins, sclerites, cross veins and brace are as defined by Kukalová-Peck, 1983, 1991, 1997; Kukalová-Peck & Lawrence, 1993; and as presented in an improved version in this account (Figs 1A, 1B; Table 6). Note that the higher-level characters of wings as mentioned in the table cease being informative at about the family level and below.

TABLE 6A. Character state distribution in Protowing, Neoptera and Palaeoptera.

Protowing characters (ancestral to clades 1, 0) all coded as 0	Clade 1. Neoptera (Fig. 1)	Clade 0. Palaeoptera
Kukalová-Peck, 1978; Kukalová-Peck & Brauckmann, 1990; Wootton & Kukalová-Peck, 2000	Kukalová, 1964a; Kukalová-Peck, 1978, 1983, 1991, 1997; Brodsky, 1994	Kukalová-Peck, 1978, 1983, 1985, 1991, 1997; Brodsky, 1994
Flight, Folds, Wing Flexing		
Protowings, as recorded on fossil prothoraces: mobile, membranous with dense irregular cross-veins, anterior margin formed, veinal sectors fluted, articular sclerites form short, arched welt	1 – prothoracic wings immobilized, veins reduced; later fused with tergum into prothoracic shield, many times in parallel	0 – present (in fossil odonatoids Geroptera & Palaeodictyoptera); later veined, diminished, in Ephemeroptera stem line, or fused with tergum into prothoracic shield, or lost
Meso- & metathoracic protowings: both pairs almost equally wide	1 – heteronomous: forewings narrow, hindwing with broad anojugal lobe; later hindwings diminish repeatedly, in parallel	0 – homonomous; later hindwing somewhat broader near base or reduced, or petiolate, repeatedly in parallel
Meso- & metathoracic protowing pairs, arrangement of veins: homonomous & radial	1 – heteronomous, anal area in forewings asymmetrical, adapted for locking them in flexed position	0 – wing pairs homonomous, with radially arranged wing venation
Membrane: rather thick with dense, irregular cross-veins, in both protowing pairs	1 – heteronomous, forewings tegminous, hindwings thinly membranous with weak irregular cross-veins	0 – homonomous, both wing pairs membranous with dense, irregular cross-veins
Fore- & hind protowing pair: similar function	1 – heteronomous function: forewings protecting & flying, hindwings principal flying pair	0 – homonomous function, both pairs flying
Wing flexing: protowings are pulled closer to body & warped (in nymphs of Diaphanopterodea only)	2 – 3Ax pivots, collapses into a membranous window, pulls on three arms articulated with BCu, BA, BJ & fold wing veins	1 – gaps between rows of sclerites Cu, A, J close, pliable veinal bases bend, wigs flex (in adult Diaphanopterodea only)

Protowing characters (ancestral to clades 1, 0) all coded as 0	Clade 1. Neoptera (Fig. 1)	Clade 0. Palaeoptera
Position of protowings flexed backward: half-closed in all three thoracic wing pairs (as in nymphs of Diaphanopterodea)	0 – flexed wings held mildly roofwise in half-closed position (in fossil hemipteroids: Paoliidae only); later overlap apically, partly, or completely	0 – mildly roofwise, half-closed (in basal adult Diphanopterodea only); later overlap in derived representatives (Kukalová-Peck & Brauckmann, 1990)
Folds: uncertain	2 – folds run in membrane between veinal sectors	1 – wing flexing folds cross veinal bases (in Diaphanopterodea only); later wing flexing lost in all other Palaeoptera, (twice independently)
Medial fold absent	1 – medial fold present	0 – absent
Claval fold absent	1 – claval fold present	0 – absent
Anal fold absent	1 – anal fold present	0 – absent
Jugal fold absent	1 – jugal fold present	0 – absent
Venation in protowing	**Venation in forewing**	**Venation in forewing**
PC strip: thick, separated from CA by a suture	0 – thick; later PC expands into epipleuron (in Hemiptera, again in Coleoptera)	1 – PC strip narrow, sclerotized, serrated; later serration lost in many living Ephemerida
Costa (C): CA+ and CP- run in parallel to each other, fuse into C beyond mid-wing	0 – same (in Hemiptera, Coleoptera); later CP- fuses with CA+ close to base	1 – CA+ and CP- run in parallel in basal third of the wing (in many fossils); later they fuse into C close to base
Anal lobe not enlarged	0 – same	0 – same
Anal veins, arranged: radially, spaced in regular intervals, in both protowing pairs	1 – heteronomous: AA1+2 shifted anteriorly, distanced from AA3+4; AA3+4 & AP fused basally (radially arranged veins in hindwings)	0 – homonomous, radially arranged veins in both wing pairs
Locking devices to hold protowings in warped position: probably absent	1 – long anal bar locks on itself; later it locks on scutellum or on articular sclerites	0 – locking device absent
Jugal lobe: regular size in both protowing pairs	2 – heteronomous size: jugal lobe much shorter than anal lobe (regular size in hindwings)	1 – strongly diminished, homonomous in both wing pairs
Jugal lobe membrane: not different from other areas	1 – thinner than in the rest of forewing	0 – not different
Remigium & anal & jugal lobe: all positioned at one plane	1 – heteronomous position: remigium & anal lobe at one, jugal lobe at another plane	0 – homonomous position: at one plane
Venation in protowing	**Venation in hindwing**	**Venation in hindwing**
Veins arranged: radially	0 – radially	0 – radially
PC strip: thick, separated from CA+ by a suture	0 – same; later PC strip narrow, fused into anterior margin, or expanded into anterior lobe in Dermaptera & Coleoptera	1 – PC strip narrow, sclerotized, serrated, separated by suture from anterior margin; later serration lost in most Ephemerida
Veinal areas: placed at one plane	0 – same	0 – same
CuP: dichotomously branched	0 – present (in Orthoneoptera, hemipteroid stem line, Fulgoromorpha, Neuroptera); later simple, or lost	0 – present (in palaeodictyopteroids only); later CuP simple in Ephemeroptera + Odonatoptera
Anal basivenale (BA): not elongated or subdivided (anal lobe regular, not enlarged)	1 – BA subdivided into three articulated subdivisions: BAA1+2, BAA3+4, BAP (anal lobe enlarged)	0 – BA not subdivided (anal lobe not enlarged)
Remigium and anojugal area: not forming two flight units (protowing does not fly)	1 – form flight units separated by claval flexion line (in Pleconeoptera + Orthoneoptera); later by anal fold in Blattoneoptera + Hemineoptera + Endoneoptera	0 – not forming flight units

Protowing characters (ancestral to clades 1, 0) all coded as 0	Clade 1. Neoptera (Fig. 1)	Clade 0. Palaeoptera
Anal area, size: regular, not enlarged	1 – anal (anojugal) lobe strongly enlarged, undulating in flight; later diminished many times, in most Endoneoptera & many other groups	0 – regular (in Diaphanopterodea); later slightly enlarged in Palaeodictyoptera or strongly diminished in Ephemeroptera + Odonatoptera
Jugal area: regular size	0 – enlarged;	1 – highly reduced
Remigium & anal & jugal area: position at one plane	0 – same	0 – same
Anal brace: absent	1 – anal brace formed by contact between two basivenalia (BCu & BAA) connected at an angle	2 – anal brace connects anal branches: (sclerotization crossing veins in Palaeodictyopteroidea; arched parts of veins in Ephemeroptera + Odonatoptera
JA, JP braches: regular, dichotomously branched	1 – branches long, further divided, widely spread	1 – branches reduced, very short, condensed
Venation in protowings	**Venation in both wing pairs**	**Venation in both wing pairs**
Veinal corrugation mild, alternating: ScA+, ScP–, RA+, RP–, MA+, MP–, CuA+, CuP–, AA+, AP–, JA+, JP–; cross-vein network also corrugated	2 – alternating corrugation always retained in: ScA+, ScP–, RA+; corrugation reduced or reversed in RP, MA, MP, CuA, CuP, AA, AP, JA, JP & in cross-vein network	1 – alternating corrugation in ScA+, ScP–, RA+, RP–, MA+, MP–, CuA+, CuP–, AA+, intercalated sectors & network; corrugation reduced in AP, JA, JP
The stem of R: absent (sectors RA, RP start independently from the radial basivenale BR)	0 – R absent (in plecopteroid & hemipteroid stem lines); later R very short in Isoptera, Coleoptera, Strepsiptera, or repeatedly longer	0 – R absent (in fossil Geroptera only); later long R formed in parallel, in derived Palaeodictyopteroidea, Odonatoptera, Ephemeroptera
The stem of R: absent	1 – derived: when formed, RA superimposed on RP	2 – derived: when formed, RA & RP fused laterally to each other
The stem of M: absent (sectors MA & MP start independently from medial basivenale BM)	0 – M absent (in all Blattoneotera + Hemineoptera + Endoneoptera); later occurs in Pleconeoptera + Orthoneoptera	1 – M (MA superimposed on MP) always present, long
The stem of Cu: absent (sectors CuA & CuP start independently from cubital basivenale BCu)	0 – absent (in Orthoneoptera only); later the stem of Cu occurs repeatedly in all lines	1 – the stem of Cu always present (CuA superimposed on CuP)
CuP: dichotomously branched	0 – branched (in Orthoneoptera, hemipteroid stem line, Fulgoromorpha); later often simple, repeatedly in parallel	0 – branched (in Palaeodictyopteroidea); later CuP simple in Ephemeroptera + Odonatoptera
Flight-important cross-vein brace arculus (mp-cua or m-cua or short fusion): absent	0 – absent (in both wing pair in plecopteroid & blattoid stem lines, Isoptera); later absent in fore wings only in Blattodea, or added in both pairs, repeatedly	0 – absent (in Palaeodictyoptera); later added repeatedly in some palaeodictyopteroids and in Ephemeroptera + Odonatoptera
Articulation in both wing pairs: Protowing condition hypothetical, coded as 0	**Articulation in both wing pairs**	**Articulation in both wing pairs**
Sclerites in the precostal row (PC) and costal row (C): free, not fused into PCC sclerites	2 – fused into PCC sclerites in all columns (PR, AX, F, B), form three composite sclerites: PRPCC, tegula (AXPCC), humeral plate (FPCC+BPCC)	1 – PC, C stay free in columns PR, AX; later fuse into PCC only in columns F, B, thus forming FPCC, BPCC (in Ephemeroptera)
PRPC separate from PRC (fusion in columns absent)	1 – PRPC+PRC fused into composite sclerite PRPCC proximally from tegula (often retained, small, very large in Strepsiptera)	0 – PRPC, PRC separate (in Ephemeroptera + Odonatoptera only); later fused into PRPCC in Palaeodictyopteroidea
Sclerites in rows Sc, R, M, Cu, A, J articulated one with another (regular arrangement, no fusions, no clusters)	2 – varied: sclerites in row Sc some articulated some fused; in rows R, M unconnected; in rows Cu, A, J articulated one with another	1 – articulated, but clustered centrally at wing base (as in Diaphanopterodea); later this triggered twice fusions into articular plates, once in Palaeodictyoptera + Megasecoptera, again in Ephemeroptera + Odonatoptera

Protowing characters (ancestral to clades 1, 0) all coded as 0	Clade 1. Neoptera (Fig. 1)	Clade 0. Palaeoptera
Sclerites arranged in four regular, aligned columns: PR, AX, F, B	1 – central sclerites highly irregular, in size, shape, alignment (oblique association connected with flexing, locking wings in resting position	0 – regular, aligned columns present
Anterior and posterior wing process absent (proxalaria PR are articulated, never fused, with tergum,)	1 – fusion present: either in anterior wing process AWP (PRScR fused with tergum), or in posterior wing process PWP (PRAJ fused with tergum), or in both, repeatedly formed	0 – fusions between PR and tergum always absent
Composite sclerites selected obliquely from several disturbed columns: absent	1 – present, include: 1Ax (PRM+AXR+AXSc+FSc), 2Ax (AXM, FR), 3Ax (AXCu, AXAJ, FCu, FA, FJ)	0 – absent
Sclerites PRSc, PRR: separate (not fused together)	0 – separate (in Dermaptera, neuropteroids); later repeatedly together in AWP	0 – separate (in fossil Diaphanopterodea, Ephemeroptera, Odonatoptera); later fused in derived Palaeodictyopteroidea
Sclerite PRCu: sclerotized	1 – PRCu occupies membranous window area; pliable, ribbon–like (in Dermaptera, large aphids); later fragmented in Neuroptera, or repeatedly lost	0 – PRCu visible in fossils & basal, large representatives of all lines; later in parallel desclerotized, visible when stained
Sclerites PRA, PRJ: not fused one to another	1 – fused into PRAJ (= 4Ax) (in Orthoptera, Hymenoptera, Coleoptera); later PRAJ repeatedly fused with tergum as PWP	0 – not fused one to another; later gradually membranized in Ephemeroptera & Odonatoptera, or fused in derived Palaeodictyopteroidea
Humeral plate: absent	1 – present, composite of four fused sclerites (FPCC+BPCC); sutures between sclerites retained in basal members	0 – humeral plate absent
Tegula: absent	1 – present, a composite of two sclerites (AXPCC) bearing sensory organ	0 – tegula absent
First axillary 1Ax, irregular oblique composite sclerite: absent	1 – 1Ax composed of PRM+AXR+AXSc+FSc separated by sutures (in Neuroptera only); later sutures variously repeatedly reduced	0 – oblique composite sclerite 1Ax absent; sclerites always arranged in regular rows & undisturbed columns
Second axillary 2Ax, irregular oblique composite sclerite: absent	1 – 2Ax contains triangular large body AXM, articulated with narrow arm FR	0 – oblique composite sclerits 2Ax absent; sclerites always arranged in regular rows & columns
Third axillary 3Ax, irregular, composite, rotating sclerite with wing flexor muscle: absent	1 – 3Ax contains goblet & heel (AXCu subdivided by hinge), saucer (AXAJ), & three arms, cubital (FCu), anal (FA), jugal (FJ)	0 – absent; sclerites always arranged in regular rows & undisturbed columns
Sclerite AXM: regular, not different from other sclerites	1 – AXM triangular, enlarged	0 – unmodified
Sclerite AXCu: regular, not subdivided	1 – AXCu subdivided by hinge, forms two lobes, larger (goblet) & smaller (heel)	0 – not subdivided
Sclerites AXA, AXJ: separate, regular, not fused	1 – elongate, fused into AXAJ (saucer)	0 – AXA, AXJ separate, regular (in Diaphanopterodea only); later repeatedly & variously combined
Sclerite FR: regular	1 – FR (2Ax arm) slender	0 – unmodified
Sclerite FCu: articulated proximally with AXCu, distally with BCu	0 – articulated; fulcalaria (F) never fuse with basivenalia (B) (it would prevent wings from flexing backward)	0 – articulated (in wing-flexing Diaphanopterodea only); later fused with BCu & variously incorporated into articular plates
Sclerite FA: articulated with two separate sclerites, AXA & BA	1 – FA articulated with fused sclerite, saucer (AXAJ) & with part of basivenale (BAA3+4)	0 – present (in Diaphanopterodea only); later FA fused with BA twice, in articular plate of palaeodictyopteroids, again of Ephemeroptera + Odonatoptera

Protowing characters (ancestral to clades 1, 0) all coded as 0	Clade 1. Neoptera (Fig. 1)	Clade 0. Palaeoptera
Sclerite FJ: articulated with AXJ & with BJ	1 – FJ articulated with 3Ax saucer (AXAJ) & with BJ	0 – present (in Diaphanopterodea only); later FJ fused with BJ twice in articular plates
Sclerite FM & FCu: separate (not fused into medial plate or into articular plates)	0 – separate (in Plecoptera, Mantodea, Coleoptera); later fused repeatedly into medial plate	0 – separate (in Diaphanoptera only); later incorporated twice into articular plates, in derived Palaeodictyopteroids, again in Ephemeroptera + Odonatoptera
Basivenal column (B): straight	1 – V-shaped	0 – straight
Subcostal basivenale BSc: subdivided into two similar sublobes separated by suture, BscA & BScP	0 – BscA & BScP present (in Blattodea, Mantodea); later sublobes dissimilar, or suture reduced	0 – present (in fossil Odonatoptera, Ephemeroptera); later sulcus lost in living representatives & again in Palaeodictyopteroidea
Sclerite BSc, length: short	1 – long, jutting proximally	0 – BSc short, not jutting
Basivenalia BR, BM, BCu, BA, BJ & fulcalaria FR, FM, FCu, FA, FJ: articulated one to another	0 – articulated (condition enabling wing flexing but preventing energy-saving gliding	1 – articulated, but B & F in a dense, hinged cluster centrally (in Diaphanopterodea only); later B & F fuse twice, resulting plates enable energy-saving gliding
Anal basivenale BA: regular (not lengthened or subarticulated)	1 – BA long, subarticulated into BAA1+2, BAA3+4, BAP (to anchor long fan of branches supporting enlarged anal lobe	0 – BA regular (in Diaphanopterodea only); later diminished, fused into articular plates, twice independently

TABLE 6B. Character state distribution in Orthoneoptera + Pleconeoptera and Blattoneoptera + Hemineoptera + Endoneoptera.

Characters: states of Neoptera ground pattern coded 0 or 1 in clades 2 or 3	Clade 2. Orthoneoptera + Pleconeoptera (Figs 14, 15, 21, 22)	Clade 3. Blattoneoptera + Hemineoptera + Endoneoptera (Figs 4–13, 20, 21, 22)
Flight, Folds and Folding		
Two flight units separated by flexion line	1 – remigium & full anojugal lobe	2 – remigium + AA & partial anojugal lobe
Anojugal lobe, veinal support	0 – full anojugal lobe supported by AA, AP, JA, JP	1 – partial anojugal lobe supported by AP, JA, JP
Anojugal lobe, size	1 – full, large (in basal Plecoptera, Orthoneoptera); later reduced in derived Plecoptera, in Embioptera, or enlarged & branches added in Orthoptera	2 – partial, moderately large (in basal Fulgoromorpha, Hymenoptera, Coleopteroids, Neuropteroids, Trichoptera); later enlarged in Blattoneoptera, or gradually reduced in most Endoneoptera
Claval flexion line (fold)	0 – deep, full length	1 – shallow, shortened
Principal flexion line/fold	1 – claval flexion line	2 – anal fold
Anojugal lobe, internal folding	1 – regularly fan-like (folds between anal & jugal branches equally divergent)	2 – irregularly fan-like (folds unsettled, may cross branches, secondary folds added)
Apical folding (apical field withdrawn into wing at rest)	0 – never formed	1 – apical folding evolved several times, in Dermaptera, some Blattodea, Coleoptera
Jugal lobe proped by secondary brace in articular membrane	1 – brace present, long, runs from postero-distal corner of metanotum to BJ	0 – absent
Wing position at rest mildly roofwise, incompletely flexed backward, wings do not overlap	1 – wrapped around body dorsally & laterally (in Plecoptera, Embioptera, Orthoptera)	0 – present (in Hemipteroid stem line & some Endoneoptera); later highly roof-like or dorsally flat, wings crossed at tips or partly or fully
Wing venation		
PC strip separated by suture from anterior margin (as in protowing)	2 – PC strip fully incorporated into anterior margin	0 – PC separated by suture; later extended anteriorly into lobe in Dermaptera, Coleoptera
Forewing, CA & CP separate, fuse far from base (as in protowing)	1 – CA & CP fused into C near wing base	0 – present, CA forms anterior margin, CP runs in parallel, fuse apically (in Hemiptera, Coleoptera only)

Characters: states of Neoptera ground pattern coded 0 or 1 in clades 2 or 3	Clade 2. Orthoneoptera + Pleconeoptera (Figs 14, 15, 21, 22)	Clade 3. Blattoneoptera + Hemineoptera + Endoneoptera (Figs 4–13, 20, 21, 22)
ScA branched, joins anterior margin far from wing base	0 – present (in plecopteroid stem line & Orthoneoptera only)	1 – ScA changed into convex, blunt, sclerotized, oblique ridge
The stem of R (absent in protowing)	0 – absent (in plecopteroid stem line only); later R arises repeatedly in Plecoptera, Embioptera, Orthoneoptera	0 – absent (in hemipteroid stem line only); later extremely short in Dermaptera, Isoptera, coleopteroids, or lengthened
The stem of M (MA+MP) (absent in protowing)	1 – always present, long	0 – always absent
Sectors MA, MP arise separately from basivenale BM (as in protowing)	1 – fused into the stem of M which forks distally into MA & MP	0 – present
Sectors MA, basal portion	2 – distinct in the fork	1 – obscured: MA joins RP or R immediately at base, entry often membranized (evident in dissections under water)
Sector MP, basal portion	2 – distinct in the fork	1 – faint/obscured (visible in Mantodea & neuropteroids only); later visible only in dissections
The stem of Cu (absent in protowing)	0 – absent (always absent in Orthoneoptera; later present in Pleconeoptera)	2 – present, very short (in Dermaptera, Isoptera; later repeatedly lengthened
AA dichotomously branched several times (as in protowing)	0 – branches broadly diverged (in Plecoptera); later number of AA branches increased in Orthoptera	1 – AA branches few, narrowly diverged; later progressively reduced, repeatedly in parallel
AP dichotomously branched (as in protowing)	0 – present (in Pleconeoptera); later number of AP branches increased in Orthoptera	0 – present (in basal Hemineoptera & Endoneoptera; later number of AP branches increased in Blattoneoptera
JA, JP dichotomously branched	0 – present	0 – present (in Blattoneoptera); later branches reduced in Hemineoptera, Endoneoptera
Embayments in posterior wing margin	0 – one, claval	1 – two, larger anal, smaller claval
Articulation		
PRSc & PRR separate	1 – AWP present (PRSc+PRR fused together & with tergum into anterior wing process)	0 – AWP absent (in Dermaptera & neuropteroids only); later often formed, in parallel
PRCu (reducing, placed in the way of collapsing 3Ax)	2 – lost	1 – present (forming a long, pliable ribbon or fragmented); later lost, repeatedly in parallel
4Ax (=PRAJ articulated with tergum); (PRAJ fused with tergum = PWP)	1 – 4Ax present (in basal Orthoneoptera only); later PWP arises many times	1 – 4Ax present (in Hymenoptera & Coleoptera: Gyrinidae only); later PWP arises many times
PWP when formed	1 – regular	2 – more or less modified (in Hemineoptera & Endoneoptera); later fully membranized in Blattoneoptera
2Ax body (AXM) triangular	1 – triangle large, strongly & fully sclerotized	2 – triangle small, curved, distally desclerotized
2Ax radial arm (FR)	1 – lid-like, about as long as the length of 2Ax body	2 – longer than 2Ax body, oriented at an angle
FM, FCu separate (as in Neoptera ground pattern: fused FM+FC form medial plate)	0 – separate (in Plecoptera); later medial plate formed in Embioptera, again in Orthoneoptera	0 – FM, FCu separate (in Mantodea, Coleoptera); later medial plate repeatedly formed
3Ax anal arm (FA) articulated with 3Ax saucer & with BAA3+4 (as in Neoptera ground pattern)	1 – present	1 – present (in Blattoneoptera only); later FA always fused with 3Ax saucer (AXAJ), in Hemineoptera + Endoneoptera
3Ax jugal arm (FJ) articulated between 3Ax saucer & BJ (as in Neoptera ground pattern)	1 – FJ lost, connection between 3Ax & BJ lost	0 – present (in basal Blattodea only); later FJ lost in derived Blattodea, fused with saucer in Hemineoptera + Endoneoptera
BSc, sublobes BScA & BScP	1 – BScA distinctly longer than BScP	0 – sublobes BScA & BScP equally long
BJ supported proximally by a long secondary strut	1 – present, secondary strut runs in articular membrane	0 – BJ not supported, strut absent

TABLE 6C Characters state distribution in Pleconeoptera (including Embioptera) and Orthoneoptera.

Characters: states of the shared ancestor coded 0 or 1 in clades 8 or 9	Clade 8. Pleconeoptera including Embioptera (JKP unpublished observation) (Fig. 14)	Clade 9. Orthoneoptera (Figs 15, 21, 22)
Flight, Folds and Folding		
Full anojugal lobe large	1 – lobe tends to diminish in derived members	2 – lobe mostly tends to enlarge in derived members
Long secondary strut in articular membrane supporting jugal lobe	1 – runs transversely in articular membrane	2 – runs close to posterior wing margin
Wing venation		
Forewing, anterior margin	1 – sclerotized	2 – desclerotized basally under tightly fitted prothoracic shield
Forewing, ScA+ before joining anterior margin (long, branched in protowing)	0 – present (in plecopteroid stem line only); later progressively simplified & shortened	2 – extra long & branched, replaced C in supporting anterior margin (C too weak under prothoracic shield)
The stem of R (RA + RP fused) (absent in protowing)	0 – absent (in plecopteroid stem line only); later R formed in Plecoptera, Embioptera	1 – present, long, strong, basally supported by M+CuA running close
Arculus, cross-vein brace mp-cua or m-cua or short veinal fusion (absent in protowing)	0 – absent (in stem line plecopteroids: Liomopterida only); later arculus added in Plecoptera, Embioptera	1 – replaced by unique, long fusion of CuA fused since base with M, then with MP, then separating apically from MP
The stem of Cu (CuA + CuP fused) (absent in protowing)	3 – Cu present, relatively long	0 – Cu always absent
Forewing, CuA deeply forked into long, branched CuA1+2 & short CuA3+4	1 – unique deep fork present (in plecopteroid stem line, Plecoptera, Embioptera)	0 – CuA branches not modified
CuP branched	1 – CuP simple, branches lost	0 – CuP branched
Branch CuP1+2	1 – regular branch	2 – CuP1+2 forms important veinal brace: in forewing between CuP & MP+CuA: in hindwing between CuP & M+CuA (JKP, unpublished)
Anal branches, number	0 – regular; later reduced	0 – number regular; later increased
Articulation		
AWP (PRScR fused with tergum)	1 – AWP present, large	2 – AWP reduced
PRAJ (4Ax, PWP)	1 – PWP present, short	0 – 4Ax present (in Acridoidea only); later PWP arises, repeatedly in parallel
1Ax, head (FSc) & neck (AXSc)	1 – 1Ax head articulated with BSc, fused with 1Ax neck (suture preserved) (as in Neoptera ground pattern)	2 – 1Ax head associated/fused with BSc, articulated with pliable 1Ax neck
2Ax, body (AXM) & arm (FR) (articulated in Neoptera ground pattern)	1 – arm lid-like, articulated with robust, triangular 2Ax body	2 – arm lid-like, partly fused with robust, triangular 2Ax body; later arm broadened in derived Acridoidea
3Ax cubital arm (FCu) (free in Neoptera ground pattern)	0 – free (in Plecoptera); later fused in medial plate, in Embioptera	1 – fused in medial plate
3Ax, anal arm (FA) (articulated with AA3+4 in Neoptera ground pattern)	1 – FA present, relatively short (in Plecoptera)	2 – FA long, runs in parallel with extra long BAA, connected with BAA by broad, flexible sclerotization
BSc with sublobes BScA & BScP	1 – BScA longer than BScP, thin, protruding strongly proximally	2 – fused into short BSc

TABLE 6D. Characters state distribution in Blattoneoptera and Hemineoptera + Endoneoptera.

Characters: states of the shared ancestor coded 0 or 1 or 2 in clades 4 or 5	Clade 4. Blattoneoptera (Figs 4–13, 20–22)	Clade 5. Hemineoptera + Endoneoptera (Figs 16, 17, 22)
Flight, Folds and Folding		
Flight powered from both wing pairs, forewings protective, hindwings main flying pair (similar as in Neoptera ground pattern with full anojugal lobe)	1 – forewings terminous, narrower, flying; hindwings main flying pair, membranous, with broad anojugal lobe	2 – forewing thinning, hindwing diminishing (basal states as in Fulgoromorpha, Neuroptera); later forewings mainly flying, coupled with smaller hindwings, in Hymenoptera, mecopteroids, or only hind pair powered in Coleoptera + Strepsiptera

Characters: states of the shared ancestor coded 0 or 1 or 2 in clades 4 or 5	Clade 4. Blattoneoptera (Figs 4–13, 20–22)	Clade 5. Hemineoptera + Endoneoptera (Figs 16, 17, 22)
Claval fold: flanked by CuP & AA1+2	1 – CuP & AA1+2 unstable (either may descend into bottom of claval fold)	0 – present; later either CuP or AA1+2 or both become reduced
Anal fold reducing, erratic	2 – anal fold weakened but stabilized, does not cross AP1+2 branches	1 – anal fold erratic, may cross AP1+2 or get adjacent to it (in Hemiptera & Neuroptera)
Hindwings with partial anojugal lobe, slightly shorter than forewings, anojugal area	2 – slightly shorter, with anojugal lobe significantly secondarily enlarged in AP area, supported by added AP branches	1 – partial lobe broad (basal states in Fulgoromorpha, Hymenoptera, neuropteroids, coleopteroids, Trichoptera); later much diminished, frequently in parallel
Partial anojugal lobe modestly broader than in forewing	2 – distal part of AP area secondarily enlarged, bears secondary twigs (compensation for AA absent from lobe) (in Dermaptera, Dictyoptera)	1 – present (in Hymenoptera, neuropteroids, coleopteroids, Trichoptera); later lobe frequently strongly diminished, narrow
Folding in partial anojugal lobe: slightly irregular fan-like, along anal, claval & other folds	3 – present (in Dermaptera, Mantodea, Blattodea); later book-like & flat in blattoid stem line & Isoptera	2 – progressively reduced & less regular (in Hymenoptera, neuropteroids, mecopteroids); later book-like along anal fold in Coleoptera
Wing position at rest: mildly roofwise, wings not crossed (as in Neoptera ground pattern)	2 – dorsally flat, wings crossed only at tips (in blattoid stem line); later partially or fully crossed	0 – mildly roofwise (in basal representatives); later highly roofwise, or dorsally flat, crossed at wing tips, partially or fully

Wing venation

Forewing, PC strip: thick, separated by suture from CA (as in protowing)	3 – integrated into anterior margin	0 – present; later PC enlarged into epipleuron (in Hemiptera & Coleoptera), or fused with anterior margin
Hindwing, PC strip: present, not integrated into anterior margin	0 – present (PC forms anterior lobe in Dermaptera); later repeatedly fully fused with C	0 – present (PC forms anterior lobe in Coleoptera); later repeatedly fully fused with C
Forewing: CA & CP run in parallel for long distance (as in protowing)	2 – CA+CP fused since base, form strong anterior margin	0 – CA, CP run separately (in Hemiptera & Coleoptera only); later CA+CP fused into C repeatedly near base
ScA+ forms a ridge	1 – ScA ridge narrow, oblique, blunted on top	2 – ridge expanded into broad, convex, sclerotized bulge
The stem of R (absent in protowing)	1 – R very short (in Isoptera); later repeatedly lengthened	0 – R absent (in hemipteroid stem line only); later very short in coleopteroids, or repeatedly lengthened
Special, flight important cross-vein brace rpma-mp	2 – present relatively far from wing base, short	1 – present near wing base, long (in coleopteroids + neuropteroids; later more distaly in mecopteroids, again in Hymenoptera
Arculus, flight important homoplastic cross-vein brace mp-cua or m-cua or short fusion (absent in Neoptera ground pattern)	0 – absent in both wing pairs (in blattoid stem line & Isoptera); later present only in hindwings in Blattodea & Mantodea, or in both wing pairs, in Dermaptera	1 – always present in both wing pairs (a synapomorphy)
The stem of Cu absent (as in protowing)	2 – present, very short	0 – absent (in hemipteroid stem line only); later repeatedly formed
CuP (branched in protowing)	2 – simple; later lost	0 – branched (in hemipteroid stem line & Fulgoromorpha only); later simple or lost
AA1+2 simple, strong	2 – simple; later lost	1 – strong (in Hymenoptera only); later lost in Hemineoptera, again in all remaining Endoneoptera
AA3+4 forks into AA3 & AA4	0 – fork present (only in Dermaptera); later simple (in Mantodea), or supported by short serial twigs (in blattoid stem line & Isoptera)	0 – AA3+4 forks into AA3 & AA4 (in Coleoptera only); later repeatedly simple

Characters: states of the shared ancestor coded 0 or 1 or 2 in clades 4 or 5	Clade 4. Blattoneoptera (Figs 4–13, 20–22)	Clade 5. Hemineoptera + Endoneoptera (Figs 16, 17, 22)
AP sparsely branched	3 – AP1+2 enriched with serial pectinate twigs added apically (in Dermaptera, Dictyoptera)	0 – AP not enriched (in Hymenoptera, coleopteroids, neuropteroids); later branches often strongly reduced
JA, JP (dichotomously branched in pro-towing)	0 – dichotomously branched	1 – branches short; later strongly reduced, in parallel
Wing articulation		
AWP (absent in Neoptera groundplan, PRSc & PRR separate, each hinged with tergum)	0 – AWP absent (PRSc, PRR free in Dermaptera only); later AWP often arises	0 – AWP absent (PRSc, PRR free in neuropteroids only); later AWP often arises
Composite sclerite PRAJ (as 4Ax when hinged with tergum; as PWP when fused with tergum)	3 – PRAJ always completely membranized	0 – 4Ax present (in Hymenoptera & Coleoptera: Gyrinidae only); later PWP formed repeatedly, often partly membranized
2Ax body (AXM) triangular, proximal margin thickened, distal part weakened	3 – 2Ax body curved, proximal margin thickened, distal part membranized & wrinkled	2 – 2Ax body triagular, partly desclerotized; later distally enlarged & domed in Hemineoptera
2Ax arm (FR) narrow	1 – FR narrow, thin, pliable	2 – FR broad, lobate
FM, FCu separate (as in Neoptera ground pattern), not fused into medial plate	1 – FM, FCu separate (in Mantodea only); later medial plate, tringular, in parallel	2 – medial plate short & broad, FM, FCu separated by suture; later suture reduced
3Ax anal arm (FA) articulated with 3Ax saucer (AXAJ) (in Neoptera ground pattern)	1 – FA articulated with saucer, narrow (in basal Blattodea); later broad in Blattodea, Isoptera, or fused into FAJ, in Mantodea, in Dermaptera	2 – FA fused with saucer & protruding (in Hymenoptera & mecopteroids); later forms only narrow rim on saucer, in coleopteroids+neuropteroids
3Ax jugal arm (FJ) (articulated with saucer (AXAJ) in Neoptera groundplan)	1 – FJ articulated with saucer (in basal Blattodea only); later repeatedly lost, or fused with FA into FAJ, in Dermaptera, again in Mantodea	2 – FJ always fused with saucer
BSc, sublobes BScA & BScP (separated by suture in Neoptera ground pattern)	1 – sublobes robust, suture distinct	2 – sublobes slender, suture weak or absent
Basivenale BM	1 – triangular, massive	2 – elongate
BM	1 – BM invaded distally by broad fold, weakened	0 – BM regular, well sclerotized, fold absent
Other		
Pronotum: shape	1 – flat & horizontal	0 – other
Position of wings when flexed backward over abdomen	2 – dorsal & horizontal, flat over abdomen, very slightly crossed apically (in stem line blattoids); later wings overlap	1 – low roofwise, half open, anojugal lobe not folded (in stem line hemipteroids: Paoliidae; later high roofwise or dorsal & horizontal or other, variously overlaped
Wing articulated with tergum at	1 – the anteriormost corner of metanotum (unique)	0 – other
Power for flight generated by regular set of muscles (as in Neoptera ground pattern)	1 – by typically transformed musculature shared by all Blattoneoptera	0 – by regular set of muscles

TABLE 6E. Character state distribution in Dermaptera and Dictyoptera.

Characters: states of the shared ancestor are coded 0 or 1or 2 or 3 in clades 13 or 6	Clade 13. Dermaptera (Figs 2, 4–10)	Clade 6. Dictyoptera (Figs 11–13)
Flight, Folds and Folding		
Remigium: length compared with anojugal lobe	1 – remigium shorter than anojugal lobe, very narrow	0 – not shorter, regular width
Apical & quadruple wing folding	1 – present	0 – absent; later apical folding in derived Blattodea
Partial anojugal lobe postero-distally enlarged	3 – present, enlargement extra large	2 – present, enlargement rather modest (in Isoptera, Blattodea); later increased in Mantodea

Characters: states of the shared ancestor are coded 0 or 1 or 2 or 3 in clades 13 or 6	Clade 13. Dermaptera (Figs 2, 4–10)	Clade 6. Dictyoptera (Figs 11–13)
Wing venation		
Precostal strip (PC)	0 – PC thick, adjacent to C (PC expands into anterior lobe)	3 – PC fully fused with anterior wing margin
Anterior margin	3 – pliable	2 – firm
Costal area (marginal area)	1– desclerotized, pliable	0 – regular
ScA+ between BSc and anterior margin	1 – ScA+ forms narrow, blunt, oblique ridge	1 – same; later ridge broadened in Mantodea
ScP	1 – reduced	0 – present
R, RA, RP, MA, MP	1 – veins simplified & condensed in narrow remigium	0 – not simplified, not condensed
The stem of Cu basally at BCu	1 – separated from BCu by a gap, proximal end pointed	0 – Cu starts from BCu
Arculus cross-vein brace (mp-cua or m-cua or short fusion) (absent in Neoptera ground pattern)	1 – present in both wing pairs	0 – absent in both wing pairs (in blattoid stem line & Isoptera); later formed only in hindwing, in Mantodea, again in Blattodea
AA1+2 present	3 – AA1+2 lost	1 – AA1+2 weak (in Isoptera & Blattodea); later lost in Mantodea
AA3+4 forked	1 – AA3+4 forked into AA3 and AA4; AA3 short, AA4 fused with AP	2 – simple (in Blattodea); later bears secondary pectinate twigs in blattoid stem line & Isoptera, or AA3+4 lost in Mantodea
AP1+2 & AP3+4 branches supporting partial anojugal lobe	3 – stabilized in derived pattern, AP1+2 8-branched, AP3 & AP4 uniquely divided	2 – AP1+2 with secondary twigs in enlarged distal part of anojugal lobe, AP3+4 regular
JA, JP branches	2 – stabilized in derived branching pattern	0 – JA, JP dichotomously branched
Articulation		
PRSc & PRR, AWP	0 – PRSc, PRR separate, each articulated with tergum	1 – AWP present (suture between PRSc & PRR retained)
PRR articulation regular (Neoptera ground pattern)	1 – PRR fused with 1Ax tail (unique adaptation)	0 – PRR regular, articulated with 1Ax waist (AXR)
Sclerite PRCu (present in Neoptera ground pattern)	0 – PRCu present, long, pliable; later membranized (like in most Pterygota)	0 – PRCu very weak (visible in basal Blattodea only); later membranized, in parallel
1Ax tail (PRM): regular	1 – massive	0 – not massive
2Ax body (AXM) curved, proximal margin thick, rest weakened & wrinkled	4 – thickened & twisted proximal margin retained, the rest lost	3 – present, 2Ax body strongly resembles an ear
2Ax arm (FR) pliable, thin, with anterior lobe	1 – arm long, lobe small	2 – arm short, lobe lost
3Ax goblet (=proximal lobe of AXCu)	2 – goblet very long & slender	0 – goblet short & robust
3Ax goblet & heel (=distal lobe of AXCu)	1 – heel cut off from goblet	0 – heel and goblet broadly connected
3Ax goblet versus saucer (AXAJ)	1 – saucer & goblet separated by membrane	0 – goblet & saucer hinged together
3Ax anal arm (FA), jugal arm (FJ): separate (as in Neoptera ground pattern)	1 – fused into unique anojugal arm (FAJ) bearing posteriorly jugal prong	0 – separate (in basal Blattodea only); later FJ reduced and FA broadened
FM, FCu separate or fused into medial plate (FM + FCu)	1 – medial plate desclerotized	0 – FM, FCu separate (in Mantodea only); later medial plate formed
BSc: sublobes BScA & BScP similar, robust, separated by suture (as in Neoptera ground pattern)	3 – BSc very long, thin, pliable, tiny sublobes retained only on its proximal tip	0 – present (in Blattodea, Mantodea); later sublobes fused without suture in Isoptera
BR, shape	1 – BR subdivided by embayment into proximal & distal lobe	0 – undisturbed, long (in Blattodea & Isoptera only); BR variously modified in Mantodea
BM, proximal margin	1 – with broad, membranized embayment	0 – undisturbed
BCu separate from BM	0 – separate	0 – separate (in Mantodea only); later fused, suture retained in Blattodea, Isoptera, or lost

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Characters: states of the shared ancestor are coded 0 or 1or 2 or 3 in clades 13 or 6	Clade 13. Dermaptera (Figs 2, 4–10)	Clade 6. Dictyoptera (Figs 11–13)
BAA1+2, BAA3+4	2 – fused, form a unique triangular plate	0 – articulated
BAP & BJ	1 – fused into narrow BAPJ	0 – BAP articulated with BJ (in Mantodea, Blattodea only); later fused in Isoptera
BAA, BAP, BJ	1 – BAA+BAP+BJ fused into uniquely shaped anojugal plate BAJ	0 – BAA, BAP, BJ articulated (in Blattodea); later fused into BAPJ in Isoptera, or BJ reduced in Mantodea
Anal brace: BAA1+2 articulated with BCu at an angle (as in Neoptera ground pattern)	2 – anal brace different: BAA triangular, overrides BCu, articulates by its distal point with BM	1 – unmodified

Table 6F. Character state distribution in Blattodea + Isoptera and Mantodea.

Characters: states of the shared ancestor are coded 0 or 1 or 2 or 3 in clades 7 or 12	Clade 7. Blattodea + Isoptera (Figs 11, 13)	Clade 12. Mantodea (Fig. 12)
Flight, Folds and Folding		
Claval fold reducing	2 – shortened	1 – long, shallow
Claval fold: reinforced by CuP, AA1+2	1 – claval fold flanked by AA1+2, which	2 – claval fold reinforced by CuP running
Folding of anojugal lobe: fan-like, slightly irregular (along anal fold & other shorter folds)	3 – present; later folding flat book-like in blattoid stem line & Isoptera	3 – slightly irregular fan-like
Wing venation		
ScA+ near wing base forms oblique ridge	1 – ridge narrow	2 – ridge broad, obtuse
ScP–	1 – short	0 – long
The stem of R (absent in Neoptera ground pattern)	1 – very short (in Isoptera only); later often lengthened	2 – R relatively long
Fusion of RP+MA: entry of MA discrete, visible in dissections, MA separates apically from RP	0 – MA visibly separates from RP	1 – MA & RP branches homogenous, MA separation discrete
MP basal portion running close to radial stem	1 – faint (in some Isoptera); later not visible in Blattodea	2 – partly visible, partly membranized by the proximo-distal fold
Arculus, homoplastic flight important cross-vein brace mp-cua (absent in Neoptera ground pattern)	0 – absent in both wing pairs (in blattoid stem line & Isoptera only); later absent in forewings but added in hindwings, in Blattodea	1 – arculus absent in forewings, added in hindwings (in parallel with Blattodea)
Boundary between distal end of Cu & base of CuA	2 – boundary not discernible (veins seems continuous)	1 – discernible (Cu can be clearly recognized from CuA)
CuP simple, runs along bottom of claval fold	2 – present (in blattoid stem line only; later CuP lost in Isoptera, again in Blattodea	2 – present, CuP runs along bottom of claval fold
AA1+2	1 – retained, simple, weak; later AA1+2 may descend into claval fold, in some Blattodea	3 – lost
AA3+4 simple, occupies narrow area	3 – area secondarily broadened, AA3+4 supported by short pectinate twigs (in blattoid stem line, Isoptera, some Blattodea)	2 – AA3+4 simple, area relatively narrow
AP area enlarged	1 – AP area secondarily enlarged, supported by secondary twigs on AP1+2	2 – AP area strongly secondarily enlarged
Wing articulation		
Humeral plate (HP)	2 – very weak	1 – regular
FM, FCu separate	1 – fused into medial plate	0 – FM, FCu separate
3Ax goblet (proximal lobe of AXCu)	2 – goblet asymmetrical, its proximal portion very robust & protruding	1 – goblet unmodified

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Characters: states of the shared ancestor are coded 0 or 1 or 2 or 3 in clades 7 or 12	Clade 7. Blattodea + Isoptera (Figs 11, 13)	Clade 12. Mantodea (Fig. 12)
3Ax anal arm (FA) & jugal arm (FJ) separate (as in Neoptera ground pattern)	1 – narrow FA & FJ present (in basal Blattodea only); later FA broadened, FJ lost, in derived Blattodea	2 – FA+FJ connected by broad, sclerotized membrane, form extra wide FAJ arm which articulates with BAP
3Ax jugal arm (FJ) articulated with 3Ax saucer & BJ (as in Neoptera ground pattern)	0 – present (in basal Blattodea only); later FJ lost in derived Blattodea, again in Isoptera	1 – FJ fused with FA, too short to articulate with BJ
BSc & ScA regular	0 – BSc & ScA not separated, regular	1 – separated by deep fold which may continue posteriorly & separate BR from R
BM & BCu separate (as in Neoptera ground pattern)	1 – BCu broadly adjacent to BM	0 – BCu slender, separate from BM (in Mantoididae only); later adjacent in derived Mantodea
BJ regular	0 – BJ sclerotized, regular	1 – membranized

TABLE 6G. Character state distribution in Blattodea and Isoptera.

Characters: states of the shared ancestor are coded 0 or 1 or 2 or 3 in clades 10 or 11	Clade 10. Blattodea (Fig. 11)	Clade 11. Isoptera (Fig. 13)
Flight, Folds and Folding		
Folding in anojugal lobe	3 – slightly irregular, mainly along anal fold	4 – lobe folds book-like flat under hindwing so that small part overlaps anterior wing margin (as in blattoid stem line)
Broad fold near wing base, posterior & parallel with R	1 – present, invades distal part of BM	0 – absent
Fold running between RA and RP near base	0 – absent	1 – present, destroys base of RP
Perpendicular fold between BM+BCu & M, Cu	0 – absent	1 – present, separates bases of M & Cu from their basivenalia
Wing venation		
Forewing: basal third	0 – regular, not diminished	1 – strongly diminished
Forewing, costal area	1 – triangular (in Palaeozoic & modern Blattodea)	0 – ribbon-like (in blattoid stem line); later strogly reduced costal area in Isoptera may be ribbon-like
The stem of R	3 – medium length, robust	1 – very short; later lengthened in blattoid stem line
RP base	0 – not disturbed	1 – membranized by crossing fold
Basal portion of MP before MP turns posteriorly towards wing margin (preserved in Mantodea)	2 – obliterated by broad fold, MP reappears at arculus	3 – cut off at BM by short fold, MP reappears distally as it turns posteriorly
Arculus, cross-vein brace mp-cua (absent in Neoptera ground pattern)	2 – absent in forewing, present in hindwing (in Palaeozoic & living Blattodea)	0 – absent in both wing pairs (in blattoid stem line & Isoptera)
The stem of Cu	3 – short	2 – very short
AA1+2 simple, reducing	1 – flanks closely claval fold, may descend into its bottom	1 – flanks closely claval fold
AA3+4, in narrow AA area associated with remigium	2 – AA3+4 simple, flanked & reinforced by strong, convex intercalary vein	1 – AA3+4 supported by serial, short & broad secondary twigs
Wing articulation		
Humeral plate	2 – weak	3 – lost
PRCu (in membranized area into which 3Ax colapses)	1 – faintly preserved (in basal Blattodea only); later membranized	2 – membranized
Medial plate	1 – present, unmodified	2 – distal margin indented
3Ax goblet, proximal portion enlarged	2 – broader than distal portion, protruding	3 – massive, highly protruding

Characters: states of the shared ancestor are coded 0 or 1 or 2 or 3 in clades 10 or 11	Clade 10. Blattodea (Fig. 11)	Clade 11. Isoptera (Fig. 13)
3Ax anal arm FA: strong	1 – strong, narrow	3 – strong, broad, massive
FCu articulated with	1 – with 3Ax heel & BCu	2 – with heel & BCu & FA (articulation with FA added)
3Ax jugal arm FJ	0 – present (in basal Blattodea only); later repeatedly lost	2 – reduced or lost
Humeral plate	2 – faintly preserved	3 – lost
BSc, sublobes BScA, BScP	1 – present, well expressed	4 – fused into uniform BSc
BM+BCu fused	1 – fused, suture preserved	2 – fused, suture lost
Anojugal basivenalia	1 – slender, convex	2 – uniquely broad & flat
BAP, BJ	0 – articulated	1 – broadly fused

Table 6H. Character state distribution in Hemineoptera and Endoneoptera.

Characters: states of the shared ancestor are coded 0 or 1 or 2 in clades 14 or 15	Clade 14. Hemineoptera (Figs 16, 22)	Clade 15. Endoneoptera (Figs 17, 22) (emendation* of previous interpretations at the end)
Flight, Folds and Folding		
Claval fold with tendency to reduce	1 – long, shallow	1 – long (in Hymenoptera); later shortened, shallow, in parallel
Claval fold reinforced by	1 – flanked by CuP (in stem line hempteroids & Fulgoromorpha only); later CuP lost, in parallel	2 – flanked by AA1+2 (in Hymenoptera only); reinforcement lost in coleopteroids + neuropteroids + mecopteroids
Partial anojugal lobe, folds	3 – folds irregular, may cross anal branches (in Fulgoromorpha); later new folds added, or folds & lobe reduced	3 – claval, anal, jugal fold active (in Hymenotera only); later lobe & claval fold reduced many times, in Coleoptera anal fold folded book-like & new short folds added
Hindwings with tendency to diminish, couple with forewings in flight	0 – coupling absent; later occurs repeatedly, in most Sternorrhyncha, Heteroptera, Fulgoromorpha, Cicadomorpha	0 – coupling absent; later occurs repeatedly, in Hymenoptera, Mecoptera, Trichoptera, Lepidoptera
Wing position at rest probably mildly roofwise & not fully flexed backward	0 – wings held mildly roofwise not overlapped (in hemipteroid stem line: Paoliidae); later highly roof-wise, or dorsally flat, variously overlaping	3 – held mildly roofwise, slightly overlaped (in neuropteroids); later repeatedly roofwise, or dorsally flat, or slightly to fully overlaped, or held vertically (in Lepidoptera)
Wing venation		
Forewing, epipleuron (PC strip when extended) directed	1 – ventro-posteriorly, obliquely under anterior wing margin (in Hemiptera)	2 – mainly ventrally (in Coleoptera)
Forewing, CA+, CP– long separate, run in parallel (as in protowing)	0 – present (in hemipteroid stem line, some Hemiptera); later CA, CP repeatedly fused into C near base	0 – present (in the elytra of Coleoptera); later repeatedly fused into C at wing base
Humeral vein (cross-vein brace c-scp)	0 – absent; later weakly indicated in some forewings, independently in parallel	1 – present, formed distally of ScA bulge, prominent in both wing pairs
Forewing, ScA+ forms sclerotized convex bulge	2 – bulge low; later lost, replaced by membranized fissure at base of costal area	3 – bulge high, prominent, reinforced distally by humeral vein; later reduced in narrow costal areas
Forewing: anal lobe forms pointed clavus	1 – clavus present	0 – absent
ScP with tendency to shorten, basally close to R	1 – ScP shortened: later ScP dives basally under R (in Heteroptera, Fulgoromorpha, Cicadomorpha)	0 – ScP and R basally close but separate, ScP relatively long
RA, RP separate, the stem of R absent (as in protowing)	0 – absent (in hemipteroid stem line only); later repeatedly formed	1 – present, extremely short (in Coleoptera + Strepsiptera only); later repeatedly lengthened

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Characters: states of the shared ancestor are coded 0 or 1 or 2 in clades 14 or 15	Clade 14. Hemineoptera (Figs 16, 22)	Clade 15. Endoneoptera (Figs 17, 22) (emendation* of previous interpretations at the end)
MA fused with RP at base, separates again apically, branches	3 – separation obscured, RP & MA branches look alike, cannot be distinguished one from another	2 – evident, MA convexly fluted (+) (in hymenopteroid stem line, basal Hymenoptera, Neuroptera); later MA cannot be recognized
Cross-vein brace rpma-mp expressed	2 – far from wing base, as cross-vein brace or short fusion between RP+MA and MP	1 – near base, as long sinusoid brace (in Neuroptera, Megaloptera, medial bridge in Coleoptera + Strepsiptera); later shorter & shifted distally twice, in Hymenoptera, again in mecopteroids
MP after rising from BM turns towards posterior margin (as in protowing & Neoptera ground pattern)	2 – MP first approaches R+MA, then turns posteriorly towards wing margin	1 – MP turns posteriorly (in Hymenoptera only); later MP first approaches RP+MA, then turns posteriorly, in coleopteroids + neuropteroids + mecopteroids
MP basal portion	0 – distinct in large basal members; later often very close to R & almost invisible (evident in dissections under water)	0 – distinct (only in Hymenoptera); later visible in some Coleoptera, in neuropteroids deep under R, reduced in mecopteroids (evident in dissections under water)
Arculus, cross-vein brace mp-cua or short fusion.	1 – always present (frequently homoplastic outside Hemineoptera + Endoneoptera)	1 – always present (in coleopteroids + neuropteroids + mecopteroids); later extended into long fusion in Hymenoptera
Posterior arculus, fused brace between branches MP4-CuA1	0 – absent	1 – present (in neuropteroids obscured); later arculus and posterior arculus form one continuous fused brace in Hymenoptera
The stem of Cu	2 – present, very short	2 – present, very short (in Hymenoptera, neuropteroids); later much longer in coleopteroids, again in mecopteroids
Forewing: the stem of Cu, width	0 – width regular; later widens into pointed sclerotized plate (in Hemiptera)	0 – width regular: the stem of Cu does not widen or sclerotize
CuP dichotomously branched (as in protowing & Neoptera ground pattern	0 – CuP with long, richly divided branches (in hemipteroid stem line & Fulgoromorpha); later CuP simple or lost, many times in parallel	3 – CuP weakly branched (in neuropteroids); later simple in Coleoptera, again in mecopteroids, or lost in Hymenoptera, or simple or enriched by twigs in Neuroptera
AA1+2 (in reducing AA area adjacent to remigium)	3 – AA1+2 completely reduced, lost	2 – AA1+2 simple, strong, functional (in Hymenoptera only); later AA1+2 lost in neuropteroids + coleopteroids + mecopteroids
AA3+4 branches (in reducing AA area adjacent to remigium)	3 – AA3+4 simple, branches lost	1 – AA3+4 branched (in Neuroptera + Coleoptera only); later simple in mecopteroids, independently also in Hymenoptera
Partial anojugal lobe relatively large, AP sparsely branched	2 – present (in Fulgoromorpha); later lobe repeatedly strongly diminished	2 – present (in basal Hymenoptera, neuropteroids, coleopteroids, Trichoptera); later lobe reducing
Articulation		
Forewing, humeral plate & BSc separate	1 – connected by conspicuous, broad sclerotization	0 – separate
PRSc, PRR separate (as in Neoptera ground pattern)	1 – fused with tergum into small AWP	0 – PRSc, PRR separate, hinged with tergum (in basal Neuroptera only); AWP repeatedly formed
PRAJ (hinged with tergum = 4Ax; fused with tergum = PWP)	1 – PRAJ modified, eroded; later desclerotized, or PWP formed, or PWP desclerotized	0 – 4Ax present (in Hymenoptera & Coleoptera: Gyrinidae only); later PWP in neuropteroids, Coleoptera, again in mecopteroids
PRCu (sclerite in membranous window)	1 – present, long, pliable (in large aphids); later membranized	2 – present, fragmented (in some Neuroptera only); later lost
1Ax	2 – head & neck strongly reduced	1 – unmodified

Characters: states of the shared ancestor are coded 0 or 1 or 2 in clades 14 or 15	Clade 14. Hemineoptera (Figs 16, 22)	Clade 15. Endoneoptera (Figs 17, 22) (emendation* of previous interpretations at the end)
Forewing, 2Ax body distally weakened	1 – body distally enlarged, lobate; later sclerotized, lobes articulated with FR & FM (in Heteroptera, Fulgoromorpha, Cicadomorpha)	0 – present; secondary enlargement & sclerotization of 2Ax body absent
2Ax body (AXM) proximally stronger, distally weaker	6 – 2Ax body bears proximally thick, strongly curved rim, distal part very weak	2 – 2Ax body forms distorted, distally weakened triangle
2Ax arm (FR) broad, lobed towards BSc	2 – FR lobed twice, towards BSc & towards medial plate	1 – FR lobed only towards BSc
FM, FCu separate (as in Neoptera ground pattern)	0 – FM & FCu close but separate, not modified; later fused in medial plate, with or without dividing suture	1 – separate, modified (lost in Hymenoptera; FM subdivided, FCu fused with 3Ax in Coleoptera + Strepsiptera); later medial plate formed in neuropteroids, reduced in mecopteroids
3Ax goblet & heel (two lobes of AXCu)	1 – heel small, separated from goblet; later enlarged in Heteroptera & Fulgoro- morpha	0 – heel small, connected to goblet
3Ax saucer (AXAJ) proximally longer than goblet	1 – the proximally protruding part of saucer reduced	0 – saucer strongly protruding proximally; later it repeatedly evolved secondary hinge
anal arm FA fused with saucer, protrudes to articulate with BAA3+4	1 – present, FA forms strongly sclero- tized ridge protruding from saucer & articulated with BAA3+4	1 – present (in Hymenoptera, meco- pteroids); later FA blends into narrow rim on saucer which is connected with basive- nalia by narrow strips of tough membrane (in coleopteroids + neuropteroids)
FJ: fused with saucer, articulated with BJ	1 – articulation with BJ weak; later lost	2 – direct contact with BJ lost; later scler- ites connected by strips of toughened mem- brane in coleopteroids + neuropteroids
BR & BM separate (as in Neoptera ground pattern)	1 – broadly adjacent	0 – separate
BM & BCu separate (as in Neoptera ground pattern)	0 – BCu, BM separate	1 – BM hinged/fused with BCu

* **Emendation.** In Table 6H, important improvements in homologization in the hindwing of Coleoptera (Kukalová-Peck & Law- rence 1993, Fig. 12) are proposed as follows. MA joins R immediately at wing base and MA entry is membranized; medial bridge is a structurally important cross-vein brace rpma-mp, involved in apical folding; cubital stem is present, long; CuA forks into CuA1+2 (marked as "CuA") and CuA3+4 (marked as "CuA2"); CuP (marked as "CuA3+4") is present; AA1+2 is lost; AA3+4 forks into AA3 (marked as "AA1+2") which is braced with CuP, and into AA4 (marked as "AA3+4"); arculus is mp-cu (marked as "mp-cua"); the veinal fusion near the posterior margin is MP4 + CuA1+2 (marked as "MP4 + CuA1"). The changes will be dis- cussed and documented in soon to be published paper by the same authors.

Other improvements of full homologizations in Neoptera previously offered by Kukalová-Peck (1991 and elsewhere), discussed here and introduced in Table 6, are shown in figures of the representatives of living superordinal lines. Broader documentation and discussion will be presented later, when the pterygote superorders will be dealt with individually (in advanced preparation by JKP).

The data set is focused on interpreting the phylogenetic position of Dermaptera within the Pterygota. Orders within Palaeoptera and outside of Blattoneoptera are not fully characterized here. For that reason, the character table is not complete enough for a cladistic analysis of Neoptera. It is also open to further improvements as research on the ordinal ground patterns proceeds.

Unless the forewing is specifically mentioned, **all char- acters concern only the hindwing.**

As customary, the numeral **0 is plesiomorphic; 1 through 6 represent unordered apomorphic states.**

Protowing ground pattern (Kukalová-Peck, 1978, 1983, 1985, 1991; Wootton & Kukalová-Peck, 2000). In the ancestral protowing ground pattern hypothesis there are 8 principal veins (PC, C, Sc, R, M, Cu, A, J). All except PC (precostal strip) are preserved as two corru- gated sectors, anterior (A) convex (+) and posterior (P) concave (–). All sectors except CA (forming costal mar- gin) are dichotomously branched about 3 times. Articular sclerites are aligned with their veins in 8 rows (PC, C, Sc, R, M, Cu, A, J), and are arranged in 4 columns (PR, AX, F, B).

The pterygote protowing is almost perfectly retained in the **prothoracic wings** of Palaeodictyoptera and extinct Odonatoptera (Geroptera). It is supported by the costal margin (a fusion of PC strip and CA) and by radially arranged veins. Each principal veins composed of two veinal sectors: anterior – convex and posterior – concave.

Veinal sectors are dichotomously branched, mildly corrugated, and connected by numerous, irregular cross-veins. The prothoracic protowing is slightly asymmetrical, with veins crowded anteriorly towards the costal margin. Articular sclerites are present, but are fused into a composite, arched welt. Secondary reductions include diminished branching. These features show that prothoracic protowings were previously adapted for flapping forward movement of some sort, but became gradually less active and were in the process of reduction.

However, powered aerial flight was definitely not a function of protowings. This requires a much larger size; denser anterior crowding of veins; the presence of an anal brace; fusions of veins into veinal stems or braces near the wing base; a twist-promoting wing articulation; and a specialized and well-coordinated thoracic and limb musculature, manipulating wings by pulling on articular sclerites. These adaptations took place in Pterygota in two profoundly different styles, which are here recognized as the pterygote clades Neoptera and Palaeoptera (Kukalová-Peck, 1978, 1983, 1991, 1997).

Pterygota and monophyly. Pterygota are monophyletic. We know of no evidence to the contrary. Consequently, all characters in all orders must be interpretable from a single protowing ground pattern of venation and articulation. Only one nomenclature must be used for all orders to obtain valid answers about their phylogenetic relatioship. It is very well documented that all representatives, extinct and extant, always share an identical ground pattern of stabilized order-level character states. As a clade evolves, new transformation (mainly reductions, fusions and extensions) will be added in the subtaxa (suborders, families, genera and species). These may obscure, but will not change, the ground pattern of their order. Consequently, the ordinal character states are predictably present, can be recognized and assembled in a ground pattern. They are those characters, which are shared by all representatives of the order. The stability of the wing complex means that the principal veins and articular sclerites, which in ground pattern are fused together in stems and composite sclerites, or lost, never unfuse or reappear in any extinct or extant representatives of an order. Fusions, reductions or losses will gradually accumulate, but not oscillate, because there is no evidence, ever, of reversals at the ordinal level (see numerous examples below).

In the wing character complex, the ground pattern can be convincingly presented only if compared with an ex-group: In Neoptera, with Palaeoptera; in Blattoneoptera, with other superordinal lines; in Dermaptera, with other blattoid orders, etc. In Pterygota, the task of full homologization is multi-layered and almost overwhelming but nevertheless absolutely necessary, because it provides the way to recognize seemingly "unrecognizable" homoplasies. As a fact, almost all (!) higher-level characters are multi-homoplasious, simultaneously in related and unrelated orders and/or in their subtaxa. The only way to avoid chaos is to use each time, in the Pterygote superorders and orders, only the fully homologized ground pat-

terns. To let synapomorphies stand out, the order-level characters must be handled strictly within the context in which they occur. Table 6 presents many self-explanatory examples of previously "unrecognizable" homoplasies, which can be recognized instantly in a proper context. These are mentioned after the word "later". They show the range of homoplastic diversifications, and the astonishing quantity of homoplasies in unrelated taxa, which must be excluded from cladistic analysis.

It is important to note that all character states in the Table 6 are at the ground pattern level of the clade. Any later transformations are irrelevant to phylogenetic consideration and must be excluded from consideration. The character table deals with an exceptionally rich and unevenly changing character complex. We have tried to present the characters in the most concise and manageable way possible, while also pointing out homoplasies. The goal is to document convincingly the theoretical thesis of this paper, namely that any phylogenetic analysis of an order using morphological character complexes must include homologization of all orders of the respective higher taxon, all the way back to the shared ancestor. In the wing complex, it is the protowing of the ancestral pterygote. In a limb-derived appendage, it is the limb of the ancestral Proterozoic arthropod. We expect that in future wing character tables it will not be necessary to deal so much with homoplasies once this current problem is out of the way.

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