

A Modified Paranotal Theory of Insect Wing Origin

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ABSTRACT The theory of Kukalova-Peck ('78) is examined and rejected except for the hypothesis of the partially pleural origin of wings. Data suggest that the arthropods ancestral to insects left the water, and that movable precursors of the wings, possibly exopodites, were immobilized and fused with the tergum to form part of the complex paranota. Later, during insect adaptation for flight, parts of the complex paranota were separated secondarily and became wings.

The old and widely accepted paranotal theory of the origin of wings in insects has lately been subjected to a well-reasoned critique by Kukalova-Peck ('78). Rejecting the origin of wings from a paranotum, i.e. the free marginal fold of a tergum (more precisely from its postero-lateral part), she has developed her own theory of wing origin which may be summarized as follows.

A wing is of pleural, not of tergal origin and is an appendage of the subcoxa, serially homologous to the abdominal gill-plates of Ephemeroptera (= Ephemeridia¹) nymphs and to those of adults and nymphs of certain paleozoic Protorthoptera (= Grylloblattida²). Movable pro-wings with complex articulation, obvious venation and distinctly corrugated surface existed long before the origin of flight. These may have been inherited from primary aquatic arthropods ancestral to insects. Only much later, after flight had evolved, did the temporary fusion of wings with tergum occur in the preimaginal stages as an adaptation to movement within shelters, among plants and so on. This fusion was thus a response to selection for streamlined body shape. The functions of these preflight wings were assumed to have been quite diverse: ventilation or closing of spiracles, retaining water essential for respiration during a period of absence from water, gill protection and ventilation in water, and touch, or locomotor function (as a fin). Transition to flight occurred in the late Silurian or Early Devonian during an amphibious phase, the insects climbing into trees to feed, copulate and disperse. Flapping flight was present from the very beginning, although gliding flight was presumably used simultaneously to save energy. Palaeoptera appeared first and were the ancestors of Neoptera. The main features of Palaeoptera—wings not folded back over ab-

domen at rest, straight hinge line and complete corrugation (initially with alternating six convex and six concave main veins)—are primitive. The backward wing and wing-pad position appeared independently in palaeopteran nymphs, in the imagines of the palaeopteran order Diaphanopteroidea (= Diaphanopterida) and in both the imagines and nymphs of Neoptera. This position was achieved in a different way in each taxon by bending of the wing base in palaeopteran nymphs and by rotation around the shifted third axillaries in both nymphs and imagines of Neoptera. The details of wing folding in Diaphanopterida are unknown.

Several other problems are considered by Kukalova-Peck (e.g., the origin of metamorphosis, irreversibility of evolution and taxonomic implications), but only wing and flight origin in insects will be discussed here. According to her hypothesis, the pleural nature of the insect wing seems to be well supported by the fact that in insects belonging to several different orders a wing anlage appears above the spiracle independently of the tergum and only later migrates toward the lateral tergal margin to become incorporated into paranota. The latter are thus of complex nature (Bocharova-Messner, '59, '65, '68, '71). This hy-

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1. The new, rationalized names of higher insect taxa are used here, following or followed by the traditional names when necessary. The nomenclatural reforms proposed by Rohdendorf ('77; Rohdendorf and Rasnitsyn, '80) consist of extending the nomenclatural rules concerning the names of family groups to all higher taxa. The advantage of using these rules is confirmed by the history of zoological taxonomy.

2. Jurassic fossils described by Rasnitsyn ('76a) filled the hiatus between living Grylloblattidae and extinct Megakhosaridae. Therefore, Grylloblattidae must be lumped with Protorthoptera as interpreted by Kukalova-Peck and others, but excluding Paoliidae, Sthenaropodidae and some other families (see Rohdendorf and Rasnitsyn, '80, for details).

pothesis seems especially tempting, as it permits continuity in the evolution of insect wings as locomotory organs, i.e. the wing can be considered as a homologue, full or partial, of the proepipodite (a movable appendage of the sub-coxa) in an aquatic arthropod ancestral to insects. The homology of wings (not legs) and gill-plates in mayflies and some aquatic Grylloblattida also seems to be reliable.

Permanent mobility of pro-wings during early stages of insect evolution was considered to be adaptive in water (Kukalova-Peck, '78), but that opinion is not supported by paleontological evidence. With the exception of those embedded in amber, fossil insects were buried in water deposits; therefore chances of fossilization were much higher for aquatic and amphibious insects than for terrestrial ones. Unquestionable remains of aquatic forms appear much later (early Permian), however, than those of terrestrial forms (Namurian age, at the very beginning of the late Carboniferous in the North American geochronological scale).

The way of life of the winged insect ancestors reconstructed by Kukalova-Peck ('78) and Mamaev ('75) also testifies against water as the habitat of "pre-apterygotes". If the latter climbed trees to feed, copulate and disperse, why would they return to water, a habitat much more frequented by predators, parasites and pathogenic agents than is land?

It seems probable that insects have evolved instead as a terrestrial group. Occupation of aquatic habitats probably came later, after they had evolved flight. The movable abdominal pro-wings (gill-plates) present in the nymphs of mayflies and Lemmatophoridae (Grylloblattida) should thus be considered secondarily developed. Reappearance (secondary detachment) of external structures, which have fused or otherwise seemingly disappeared in certain ancestral lines, is often observed in the phylogeny of insects, because rudiments of

such structures are usually present at proper developmental stages (Tichomirova, '76).

Upward migration of abdominal pro-wing (gill-plate) anlagen during ontogeny presents additional evidence contrary to Kukalova-Peck's hypothesis of pro-wing mobility. She postulated a similar migration in thoracic wing anlagen as being required to attach the wing functionally to the tergum. This explanation, however, can hardly be valid for mayfly gill-plates, which do not need as firm an attachment as flying wings do. This pattern of development of the gill-plates compels a search for a common reason for migration of gill-plates and wing primordia. The explanation proposed by Kukalova-Peck ('78) is that selection for streamlined body shape caused fusion of the wing-pads with paranota. Selection for streamlined body shape and for free movement in water and in habitats with obstacles surely occurred in Insecta generally, however, and not merely after the origin of flight. Pro-wings might be expected to fuse with paranota when they lost their primordial function (respiration and/or swimming), at the time or shortly after the remote insect ancestors were leaving the aquatic habitat.

The assumption that insect paranota are of complex nature, consisting of tergal as well as pleural components, allows reconciliation of the hypotheses of both pleural and paranotal origin of the insect wing. Kukalova-Peck considers this to be impossible, because she believes that the nymphs of paleozoic insects had permanently movable wings during their entire ontogenetic and phylogenetic development. In her opinion, outstretched wing position at rest in both nymphs and imagoes phylogenetically preceded their backward position.

Mobile nymphal wing-pads did occur in some paleozoic insects, but the evidence for wing-pad mobility in their earliest nymphs does not

Fig. 1. Younger nymph of *Narkemina angustata* Martynov (Grylloblattida) with the immovable wing pads (w). Upper Carboniferous (Stephanian), Tunguska Basin, Tshun'a Riv., Coll. Paleontological Institute, Academy of Sciences of the USSR, Moscow, no. 3115/280. $\times 6.1$.

Fig. 2. Older nymph of *Narkemina angustata* Martynov (Grylloblattida). Moulding cast of pterothorax with the movable wing pads (w). The same locality and collection as in Figure 1, no. 3115/264. $\times 6.1$.

Fig. 3. Nymph of *Liomopterites* (?) *gracilis* Sharov (Grylloblattida) with the immovable wing pads (rudimentary hinge is marked by arrow). Upper Permian, Kuznetsk Basin, Kaltan vill. The same collection as in Figure 1, no. 1193/853 (holotype). $\times 11.4$.

Fig. 4. Nymph of *Liomopterites* (?) sp. with the movable wing pads (w). The same locality and collection as in Figure 3, no. 1197/846. $\times 13.0$.



seem sound. The nymphs shown by Kukalova-Peck ('78, Figs. 6, 22, 24, 28, 30, 31, 33, 35) have wing-pads subequal to longer than tergal width, thus corresponding to the last nymphal instars of modern insects. These fossil nymphs could hardly represent the early nymphal instars of these insects.

MATERIALS AND METHODS

Fossil insects from the collection of the Paleontological Institute, Academy of Sciences of the USSR, Moscow, were studied. The methods were ordinary: observation under stereoscopic microscope MIIС -2 with magnification $\times 12.5-50$, using oblique illumination. Polarized illumination or moistening the specimen with alcohol were used in order to enhance visibility of the chitinous parts. Photographs were made without polarization or moistening, using the same microscope.

OBSERVATIONS AND DISCUSSION

We lack reliable information on early stages of wing formation in immature stages of paleozoic insects, although intermediate stages are available for some forms. The relatively young nymphs of the Upper Carboniferous grylloblattid *Narkemina angustata* Mart. with short wing-pads (little longer than thoracic width) possessed only rudimentary articulating structures that were apparently immobile (Fig. 1). In mature specimens (Fig. 2) these articulating structures are more obvious and perhaps movable. Similar stages of wing development are visible in nymphs of Late Permian Grylloblattida: *Liomopterites* (?) *gracilis* Sharov (Fig. 3) and *L.* (?) sp., a paratype of the former species which cannot be conspecific with the holotype because of subequal size in spite of the different degree of wing development (Fig. 4). The wide, short wing-pad of *Kaltanympha thysanuriformis* Sharov is also of interest (Fig. 5). Its axillary apparatus and basal furrow are quite obvious, but because they occupy a minor portion of the borderline between wing-pad and tergum the wing-pad must have been immobile. The long wing-pads of older grylloblattid nymphs were movable in

all known cases, having narrow bases and differentiated basal structures; this mobility would be secondary ontogenetically and most probably also phylogenetically.

The conclusion that at some evolutionary stage the pro-wings were incorporated into the paranota to form posterolateral expansions requires the flapping flight of insects originated from gliding flight, which is the only flight type possible with expanded but immobile paranota. Kukalova-Peck considers this transition impossible, as these two mechanisms are basically different, and the transition from obligatory gliding to flapping would not be selected for. However, the mobility of a gliding surface is useful in gliding control and, once acquired, opens the way to flapping flight. Examples of such a transition do exist. An old hypothesis on the gliding flight of an avian ancestor has recently been confirmed (Rautian, '78), and a close evolutionary relationship between Chiroptera and Dermoptera suggests that bats were also derived from gliding ancestors.

Kukalova-Peck argues that Palaeoptera are more primitive than Neoptera because (1) the lateral position of wing anlagen in developing insects resembles the position of wings in adult Palaeoptera, (2) wing articulation is modified in Neoptera, (3) wing folding is different in Neoptera and Diaphanopterodea, and (4) the organization of the palaeopteran articulation apparatus and of the wing itself is more regular. This view overlooks the difficulties that insects with permanently outstretched wings would have in moving freely on plants and soil unless flight were their only mode of locomotion. Freedom of movement is possible only for very good fliers which might choose not to fold their wings. It would not be possible for the first flying insects, which possessed weak flight and had to fold their wings (Rasnitsyn, '76b, '80).

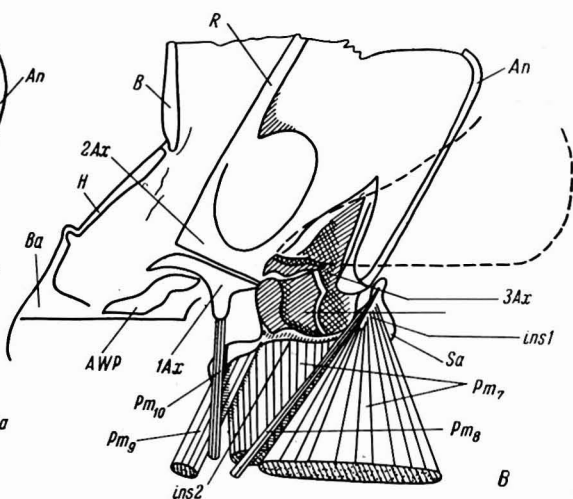
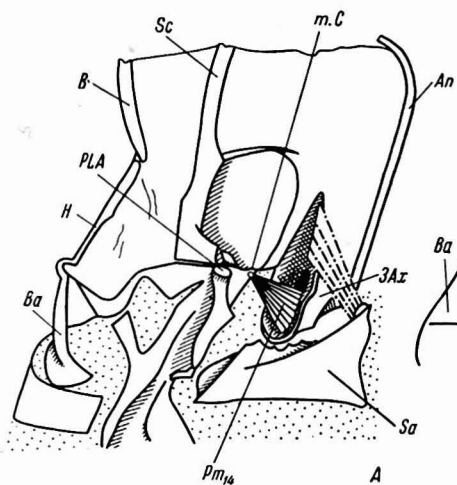
Kukalova-Peck ('78) has not discussed the implication of her hypotheses, that the primitively outstretched wings and inherited mobility of wings are mutually exclusive. Structures such as mayfly gill-plates indicate that the wing precursor already could possess an

Fig. 5. Nymph of *Kaltanympha thysanuriformis* Sharov (Grylloblattida) with the immovable wing pads (w, rudimentary hinge is marked by arrow). The same collection and locality as in Figure 3, no 966/85 (holotype). $\times 10.7$.

Fig. 6. Nymph of *Paimbia fenestrata* Sinitshenkova (*Dictyoneurida*). Moulding cast of metanotum with the wing pad. Upper Carboniferous (Stephanian). Tunguska Basin,

Paimbu Riv. The same collection as in Figure 1, no. 2993/7. After Sharov ('73). $\times 4.4$.

Fig. 7. Drawing of wing base of *Ephemera vulgata* L. (Ephemera). A. External view. B. Internal view. Ba, basallare; Sa, suballare; H, humeral plate; B, costal brace; PLA, columella; mC, posterior wing process; AWP, anterior wing process; pm, pleural muscles; ins1-2, insertions of pm. After Brodsky ('70).



articulation complex enough to ensure somewhat horizontal movements. This articulation could be easily developed further to make possible back-folding of the wing.

Evidence for different mechanisms of streamlining body shape in nymphs of Paleoptera (bending of the wing base) and Neoptera (wing-pad rotated around the third axillary shifted in a pivoting position, as in the imago) does not seem sound. Of several examples given by Kukalova-Peck, only the peculiar nymphs of Mischopterida (= Megasecoptera) have obvious signs of such bending. In other examples the curvature of the wing base, if judged by the direction of the veins, is about the same in nymphs of paleozoic Palaeoptera and Neoptera.

The difference in the articulating region of paleopteran and neopteran nymphs described by Kukalova-Peck ('78) is also not obvious. She writes that "the deep groove along the wing base of the palaeodictyopteran nymphs is the paranotal sulcus", while "the shallow grooves along the base of the neopteran wing-pads, . . . are either the mesial limits of the movable wings, or the lines of fusion between the wing and the tergum along the anal area" (*op. cit.*, pp. 61-62). I am unable to find any difference between these variants (cf. Figs. 2, 4, 6). The identification of articulating sclerites and differences in their arrangement are discussed below.

The lateral position of wing anlagen in the young of modern insects does not identify the primitive wing position positively. It may well prove to be a recapitulation, although not necessarily that of the primary wing position. For example, it may recapitulate the position of the epipodite of the remote aquatic arthropod ancestral to insects.

Kukalova-Peck's ideas on the evolution of wing articulation and venation are also open to criticism. Structure and shape of the axillary region vary so much that identification of sclerites is difficult even in living insects. Kukalova-Peck ('78, Fig. 45A) reconstructed the wing bases of two unnamed homiopterid Dictyoneurida (= Palaeodictyoptera) which were rare in their preservation, complexity and regularity of the structural elements, and arrived at the conclusion that the structure of the wing base in Palaeoptera differs markedly from that of Neoptera. This opinion is sharply contradicted by the data of Brodsky ('70, '74) who found structure, articulation and muscles of mayfly wings to be typical for Neoptera. Kukalova-Peck considered Brodsky to have misinterpreted the axillaries, claiming that his third axillary (Ax_3) was a basicubital whereas

the real Ax_3 was what Brodsky identified as the detached apex of the posterior notal process. Brodsky's interpretation (Fig. 7) is based on a thorough structural and functional analysis of mayfly wing articulation, which showed the musculature of the sclerite in question to be typical for the Ax_3 of Neoptera.

The basis for Kukalova-Peck's ideas is the hypothesis, not directly formulated, that the primary arrangement of axillaries and other elements of the wing articulation (basivenals and tergal lobes), as well as of the main wing veins, should be regular and thus that wings with the most complete and regularly arranged articulation are the most primitive. Because the wing did not necessarily originate by fusion of metamerous elements, however, its regular structure may have evolved secondarily over a long period of time. Kukalova-Peck's hypothesis is based on the assumption that articular regularity had already been attained at the time of the radiation of the winged insects. Nothing has yet confirmed this assumption; thus Brodsky's interpretation of the homology of Ax_3 remains tenable. If he is right, evidence for the distal displacement of these sclerites in Neoptera and for the different ways of wing folding in Neoptera and in Diaphanopterida then becomes invalid. In fact, a complex plate in *Permodiapha carpenteri* Kuk. encircled by a basal fold (the line of bending of the wing base at folding) and identified by Kukalova-Peck as a complex basivenalia (Fig. 8) resembles in shape and position the complex plate of a stonefly including Ax_3 (Fig. 9). It differs from a stonefly plate mostly in lacking (due to breaking off ?) a narrow base of Ax_3 and in having the base of R + M detached and crossed by basal fold. These differences are probably not of much importance.

The hypothesis of a highly regular ancestral wing venation and corrugation (with six pairs of convex, or positive and concave, or negative main veins: C +, C -, SC +, SC -, R +, RS -, MA +, MP -, CuA +, CuP -, A_1 +, A_2 -) cannot be discussed in detail, because many of the arguments have not yet been published. Here I will confine myself to a few considerations. First, the structure of the prothoracal winglet of *Stenodictya pygmea* (Kukalova-Peck, '78, Fig. 14), close to the archetype of the insect wing in Kukalova-Peck's opinion, actually does agree with this archetype (in Kukalova-Peck's sense) in the number of corrugation elements, but not in type of venation, nor in number of main veins. Secondly, wings of the Permothemistida (= Archodonata) are important for interpretation of primitive wing pattern. These highly specialized descendants of Dic-

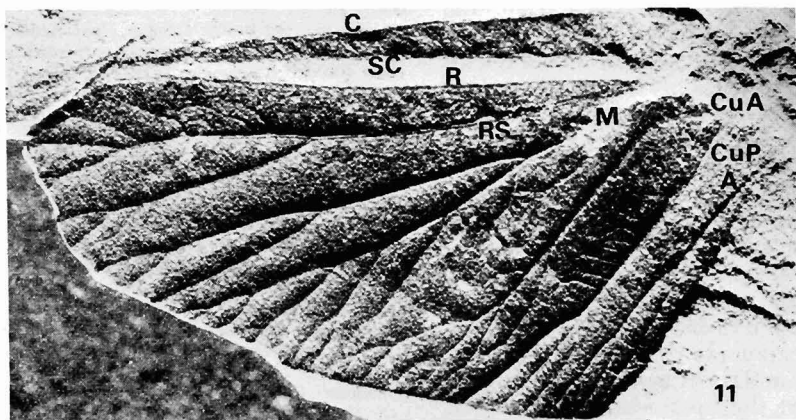
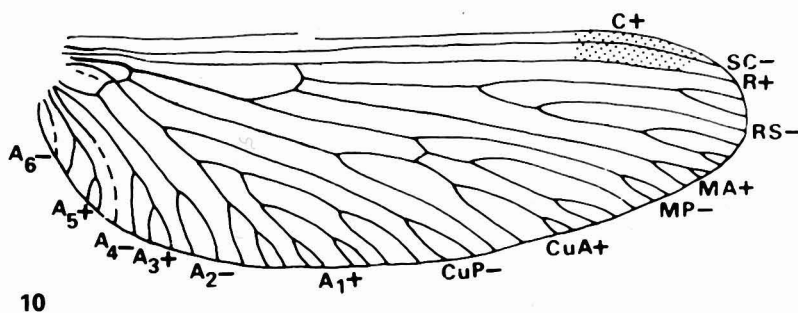
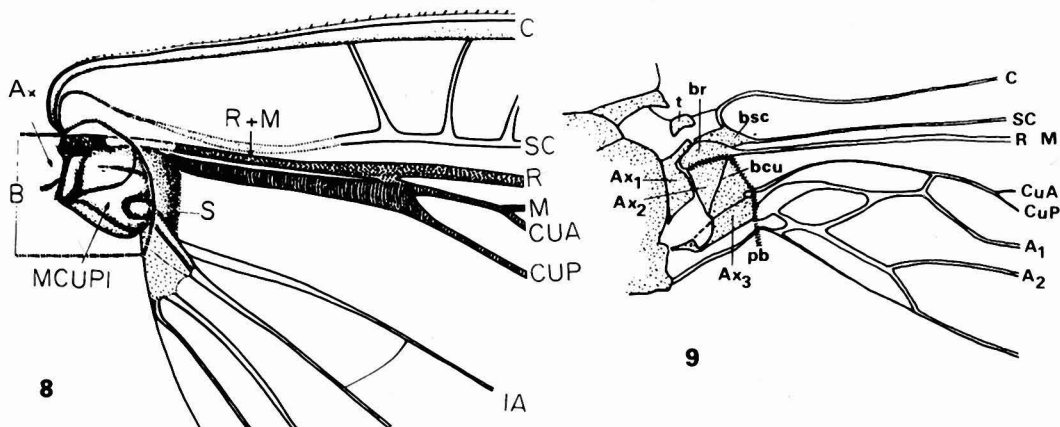


Fig. 8. Drawing of wing base of *Permodiapha carpenteri* Kukalova-Peck (*Diaphanopterida*). MCUPI, fused mediocubital basivenalia; B, basal fold. Lower Permian, Czechoslovakia. After Kukalova-Peck ('74).

Fig. 9. Drawing of wing base of *Taeniopteryx nebulosa* L. (Perlida). t, tegula; bsc, br, bscu, basivenalia; Ax1-3, axillaria; pb, basal fold, Original.

Fig. 10. Drawing of fore wing of *Permothemis libelluloides* (Martynov) (Permothemistida). Upper Permian, Archangelsk Reg., Soyana Riv. The same collection as in Figure 1, no. 2334/7 (holotype). $\times 5.6$. Original by N.D. Sinitshenkova.

Fig. 11. Hind wing of *Zdenekia* cf. *grandis* Kukalová (Paoliidae). Upper Carboniferous (Namurian). Czechoslovakia. After Kukalová ('58). $\times 2.3$.

tyoneurida have a wing corrugation much different from the scheme discussed by Kukalova-Peck and even more complex: C+, SC-, R+, RS-, MA+, MP-, CuA+, CuP-, A₁+, A₂-, A₃+, A₄-, A₅+, A₆- (Fig. 10). Thirdly, in Palaeoptera normal wing venation is the same as in Permothemistida except that all anals are convex and vary in number. In Neoptera, the pattern is basically the same except that RS and M are usually neutral. Other modifications are discussed by Rasnitsyn ('80).

A fourth consideration is that a corrugated wing surface is no doubt an ancient adaptation. It is a moot point though whether this initial corrugation was universal and regular or was partly absent as, for example, in the middle part of the wing, which was a passively deformable wing area according to Wootton ('79). Palaeontological evidence does not support the first alternative. The oldest known insects, the Paoliidae and their relatives, were dominant in the Namurian and possessed wings which were like typical neopteran wings. In their hind wings, all veins behind R were uniformly slightly concave, and corrugation was almost absent (Fig. 11). Following the fossil history of individual veins, various patterns of corrugation strengthening and weakening can be recognized. Such comparison shows a rather obvious though incomplete succession from the weak corrugation of paoliids (order Paoliida, = Protoptera) to the distinct, regular corrugation of various Palaeoptera (Rasnitsyn, '80, Rohdendorf and Rasnitsyn, '80). An almost identical corrugation in Dictyoneurida and their relatives, in dragonflies, in mayflies and in some other insects (*Homoeodictyon* Mart. for instance) has most probably been achieved independently. Such parallelism is not surprising; with intense corrugation, RS and the posterior branch of M (adhering to the convex R and CuA, respectively) became concave; and the anterior branch of M, squeezed between the now concave RS and MP, became convex.

These observations indicate that the principal evidence for unity and primitiveness of Palaeoptera is open to criticism, while numerous contrary arguments (Rasnitsyn, '69, '76b, '80, Rohdendorf and Rasnitsyn, '80) remain intact and support the involvement of the paranotum in insect wing origin. It seems probable that the paranotum for wing development originated from complex (tergal and pleural) elements.

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