

## Comment—Evolution of insect wings: a limb exite plus endite model<sup>1</sup>

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Kukulová-Peck has provided evidence that insect wings evolved from primitively moveable exite lobes of leg podomeres proximal to the coxa. Reinterpretation of previous experimental findings suggests that this hypothesis, as currently formulated, is only partly correct. The costal–subcostal field is derived from an epicoxal exite, but the radial–medial and cubital–anal fields of the wing have arisen from epicoxal endite and (or) subcoxal exite and endite lobes. Wings thus have a complex origin: limb exite plus endite.

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Kukulová-Peck a démontré que les ailes des insectes sont dérivées d'exites primitifs mobiles à la base des coxas, sur les podomères des pattes. Une nouvelle interprétation des données expérimentales déjà étudiées indique que cette hypothèse, telle que formulée actuellement, n'est que partiellement exacte. Le champ costal – sous-costal est dérivé d'un exite épicoxal, mais les champs radial–médian et cubital–anal de l'aile sont issus d'endites épicoxales et (ou) d'endites et d'exites sous-coxales. Les ailes ont donc une origine complexe et proviennent de l'évolution des exites et aussi des endites des membres.

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### Introduction

The evolutionary origin of insect wings has long been a matter for conjecture. Oken (1831, cited by Flower 1964) is credited with the first suggestion of homology between insect wings and the moveable abdominal gills of larval Ephemeroptera, but Müller (1875) was convinced that wings had a separate origin in primitively immovable outgrowths of the thoracic terga. Müller's arguments were developed by Crampton (1916), and variants of his "paranotal" model can be traced through a generation of textbooks, starting with Snodgrass (1935). Many authors, including Alexander and Brown (1963), Hinton (1963), Ross (1964), Hamilton (1971), Pringle (1974), and Douglas (1981), have sought to explain the functional significance of fixed "paranotal lobes" or the processes by which they became converted into wings, and other authors, including Kingsolver and Koel (1985), have provided information on the possible functions of primitively fixed or moveable appendages, but general agreement on the function and evolutionary development of paranotal lobes has not been forthcoming.

Nonparanotal theories have been proposed by Walton (1927), Goldschmidt (1945), and Raw (1956), each of whom attempted to derive insect wings from parts of a polychaete parapodium, but such models were never popular and can be rejected on phylogenetic grounds, unless Manton (1977) is correct in hypothesising that arthropodisation from metamerically segmented, wormlike ancestors took place on a number of separate occasions. This, however, is unlikely. Manton's logic has been strongly criticised (e.g., by Boudreaux 1979, pp. 42–45, 124–126), and her conclusions conflict with much morphological and ontogenetic evidence (various authors in Gupta 1979).

The idea that wings derive from primitively articulated structures was revived by Wigglesworth (1973, 1976), who suggested homology with the coxal styli of the Archaeognatha and serial homology with the gills of larval Ephemeroptera. Kukulová-Peck (1978, 1983, 1987) has since developed a

detailed case for the origin of wings from the moveable exite lobe of a basal leg podomere, the epicoxa, which together with a second, subcoxal podomere has become flattened and incorporated into the pterygote thoracic pleuron. In this model, serial homology with ephemeropteran larval gills is supported, but homology with coxal styli of Archaeognatha is not (Kukulová-Peck 1985). The similarly positioned, moveable larval gills of some Plecoptera are probably homologous to wings, but the paired abdominal gills of Megaloptera and of the few Odonata, Neuroptera, and Coleoptera that bear such appendages are derived from abdominal legs (J. Kukulová-Peck, personal communication). The side lobes of Archaeognatha, Thysanura, Diplura, and extinct Monura have been interpreted as fusions of the epicoxa and protowing (Kukulová-Peck 1987).

Evidence against the paranotal theory and in favour of the limb-exite origin of wings is strong. Bocharova-Messner (1959, 1971, cited by Carle 1982 and Kukulová-Peck 1978, 1983) demonstrated that the wing Anlagen originate in the pleural membrane above the spiracle and only later become associated with the tergum. Robertson et al. (1982), Dumont and Robertson (1986), and Robertson (1987) have shown that neuronal control of flight muscles involves interneurons of the first three abdominal ganglia, and, given the similarity in muscle arrangement between insect wings and ephemeropteran abdominal larval gills (Matsuda 1981), this finding suggests that the plesiomorphic condition involved a series of coordinated moveable appendages on both thoracic and abdominal segments. The pattern of attachment of the direct flight muscles (tergum–pleuron, tergum–coxa, and basalar–coxa, subalar–coxa) is as would be expected if two basal podomeres had been subsumed into the pleuron, and the tergo-sternal indirect flight muscles are readily incorporated into this scheme if the sternite is interpreted in the way that Tillyard (1926, p. 26) and Ferris (1940) suggested, as a derivative of the (sub)coxal podomere.

Kukulová-Peck (1983, 1987) has argued convincingly that the primitive arthropodan leg was an 11-segmented structure which carried a series of appendages, one exite and one endite lobe per segment, in the membranes distal to each of the more

<sup>1</sup>Papers by J. Kukulová-Peck. 1983. *Can. J. Zool.* **61**: 1618–1669, and 1987. *Can. J. Zool.* **65**: 2327–2345.

proximal podomeres. Exites and endites are primitively annulated outpouchings which do not carry intrinsic musculature but are moved from their bases by extrinsic leg muscles of the neighbouring segments. Exite lobes articulate dorsolaterally, whereas endite lobes articulate medioventrally. Many Paleozoic insects possessed four exite lobes, located on the epicoxa, subcoxa, coxa, and prefemur (the latter incorporated into the trochanter in all modern insects except larval Odonata) (Kukalová-Peck 1983), and the presence of a fifth, the trochanteral exite, has been hypothesised (Kukalová-Peck 1987). All known exite-derived structures can be attributed to one or another of these five exites. However, the number of endites required to account for previously recognised endite-derived structures is only two, the coxal and trochanteral endites (Kukalová-Peck 1987).

Kukalová-Peck's conclusion about the general structure of the primitive arthropodan leg is strongly backed by a range of fossil, phylogenetic, ontogenetic, and morphological evidence, and is fully consistent with a limb-exite origin for the wing.

### A limb exite plus endite model

Although Kukalová-Peck's model for a limb-exite origin of wings is greatly superior to any model based on the paranotal theory, it remains unconvincing on two points. First, it does not explain how an apparently simple exite lobe might develop the eight pairs of principal longitudinal veins that the model requires. Second, both Kukalová-Peck and Wigglesworth assumed that because wings articulate on the lateral surface of the thorax they must derive only from laterally articulated exite lobes. By implication, medioventrally articulated endite lobes are treated as if flattening of the podomere would have carried them to the ventral thoracic surface, where they became reduced and eliminated. In the absence of fossil evidence for intermediate stages, such an assumption is unwarranted.

The topological rearrangement required to transform cylindrical podomeres into flat pleural structures can be achieved by either of two processes. One requires a longitudinal break in the sclerotisation of the podomere, followed by flattening of the resulting surface through allometric change. The other involves shortening the podomere into a ringlike structure, which afterwards may become broken or partly desclerotised. Mixed processes are possible. There is some evidence for a two-ringed structure in the pleural, though apparently not in the sternal, sclerites of insects (Snodgrass 1935, pp. 161–166, and later authors). Whichever process or mixture of processes occurred, the result is topologically the same. There is no reason to assume that any epicoxal and subcoxal endites present in the ancestral pterygote would have been carried to the present ventral surface or would have disappeared. It is entirely possible that endite lobes would have been carried to the lateral rather than the ventral thoracic surface, or would have become located on the sterno-pleuron in a ring of membranous intersegmental tissue around which they could readily, in evolutionary time, migrate. By further allometric change, any or all of the epicoxal endite, the subcoxal exite, and the subcoxal endite could then have migrated to a position on the upper border of the pleuron close to the epicoxal exite.

### Evidence

Evidence for the origin of wings as dual structures combining both exite and endite lobe derivatives can be found in Goldschmidt's (1940, 1945, 1952) studies of the "podoptera" and

"tetraltera" homoeotic mutations of *Drosophila melanogaster*. This evidence was misinterpreted by Goldschmidt and appears to have been overlooked by later authors. Goldschmidt's (1945) *pod* mutation transforms the costal region of the wing into what looks like a three-segmented leg (described by Goldschmidt as coxa plus femur plus tibia, without tarsus). The remainder of the wing, which is separated from this structure, is small and crumpled but consists of two connected lobate sectors. The closely similar *tet* mutation (Goldschmidt 1940) produces a three-segmented structure with a swollen end like a normal haltere, and a lobate remainder. A stronger *tet* mutation, *tetraltera(Bd)* (Goldschmidt 1952) gives series in which the leglike anterior derivative is accompanied by two further parts, the first of which is often bilobed. In all cases the leglike structure is formed from the costal-subcostal region only, the first lobe of the second structure forms around the radius and medial vein, and the second around the cubitus and anal veins (vein names follow the modified Comstock-Needham system as used in Colless and McAlpine 1970). The third structure, where present, represents the allula.

Snodgrass (1935, pp. 83–86) hypothesised a three-segmented leg as being plesiomorphic for arthropods, and Goldschmidt, following this, interpreted the anterior three-segmented structure as a dorsal duplication of a whole leg. The other structure or structures he interpreted as a whole polychaete parapodium. Neither of these interpretations can be correct. Garcia-Bellido (1977) has remarked that, of the many *Drosophila* mutations recorded in the literature, Goldschmidt's *pod*, *tet*, and *tet(Bd)* are the only ones producing apparent ventrodorsal duplication of body parts. In light of Kukalová-Peck's work, it is clear that Goldschmidt's costal leglet represents the epicoxal exite, his three "segments" being annuli. The other structures seen by Goldschmidt most probably represent the "missing" endite of the epicoxal podomere, and possibly also the exite and endite of the subcoxa.

The fact that in all pterygote orders except Ephemeroptera, the costal-medial and cubito-anal-jugal regions of the wings are tracheated separately and associated ontogenetically with different spiracles (Whitten 1962) is supportive of the view that the wing may be derived from appendages of two different podomeres. On this interpretation, the monotracheate condition in mayflies must be autapomorphic, contra Kukalová-Peck (1978). It may also be of some significance that the principal line of folding in the neopteran wing, the claval fold, corresponds to the division in *pod* and *tet* mutants between the first and second parts of the second wing residual.

Further evidence in favour of a dual or compound origin of the wing can be found in ontogeny. Garcia-Bellido et al. (1973) reported that *Drosophila* wings are ontogenetically divided into three major compartments, with boundaries corresponding to the divisions between the costal-subcostal "leg" forming region, the region of the first lobe in *pod*, *tet*, and *tet(Bd)* mutants, and the remainder of the wing. This three-way structure becomes evident at about the 24- to 48-h stage. In related experiments, Garcia-Bellido et al. (1979) established the presence of an earlier or primary division into two compartments corresponding to the costal-medial and cubito-anal sections, the boundary between these being present from first differentiation of the wing disc. These findings are consistent with an ontogeny in which the wing is developed from two centres, representing two ancestral podomeres, the anterior centre further dividing into two sections during development.

## Results

An exite plus endite model for the origin of insect wings provides a better fit to existing evidence than does the epicoxal-exite model of Kukalová-Peck (1983, 1987), but conclusive attribution of wing structures to leg podomeres and identification to specific ancestral lobes is difficult. This is because the empirical evidence is largely restricted to *Drosophila*, in which a derived and highly reduced wing venation and autapomorphic construction of the thorax obscure the basic insectan pattern. On topological grounds and on evidence from *podoptera* and *tetraltera* mutations, and also from wing folding, tracheation, and ontogenetic compartmentalisation, the epicoxal exite forms only the costal-subcostal region of the wing. It can be tentatively suggested that the part of the first residual lobe in *pod* and *tet* mutations lying closest to the exite, i.e., the sector from the radius to the medial vein, may be an epicoxal endite derivative, whereas the cubito-anal sector and the allula (in Diptera), and corresponding sections in other orders, are derived from lobes of the subcoxal podomere.

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