Origin of the insect wing and wing articulation from the arthropodan leg

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The most primitive known pterygote terga, wing articulation, wings, and upper leg segments with exites, occur in gigantic Upper Carboniferous Paleodictyoptera, Homoiopteridae. Fossil features are used as clues for reinterpreting some structures connected with flight in modern Pterygota. Brief comparisons with Paleozoic Diaphanopterodea, Permothemistida, Ephemeroptera, Protodonata, and with living Ephemeroptera, Odonata, and Neoptera are given. The wing articulation of all Pterygota is derived from a common ancestral ground plan based upon features present in fossils. The ancestral wings were articulated by a closely packed band of multiple sclerites which were hinged to eight lateral tergal lobes, and aligned with eight pairs of wing veins. The axillaria of Neoptera and axillary plates of Paleoptera are composite sclerites, which originated by fusion of several sclerites of the original band. Articular patterns of Paleoptera and Neoptera evolved differently and show (*i*) the presence or absence of a gap at the cubital level, (*ii*) the presence or absence of a turning–pivoting composite third axillary sclerite (3Ax), and (*iii*) a different composition of all composite sclerites. Gliding and wing folding adaptations within the articular band are discussed. A new fossil-based interpretation of veinal stems, veinal sectors, and of their fluting near the wing base is offered. An underlying symmetry of thoracic tergal sulci, articular sclerites, and wing venation seems to point to a nearly symmetrical, nonflying pro-wing engaged in up-and-down movement. Evidence of articulation in Paleozoic nymphal wings and evolution of metamorphic instars are examined. Pitfalls of paleoentomological work are discussed. Criteria for major divisions of Pterygota are reassessed. It is hypothesized that the wing originated from the first segment (epicoxa) of the euarthropodan upper leg and its exite. An epicoxal podomere became incorporated into the body wall and broke up into an articular ring of dorsal and ventral sclerites, and an epicoxal exite flattened and became a pro-wing. The pro-wing originally operated on a row of pivots from the epicoxa and subcoxa (pleuron) and became mobilized by epicoxal leg musculature.

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C'est chez les Paléodictyoptères géants du Carbonifère supérieur, les Homoiopteridae, qu'existent, chez un ptérygote, les formes les plus primitives de tergum, d'articulations alaire, d'ailes et de segments munis d'exites dans la partie supérieure de la patte. Les caractéristiques fossiles sont utilisées pour réinterpréter certaines structures liées au vol chez les ptérygotes modernes. De courtes comparaisons sont présentées entre, d'une part, les Diaphanopterodea du Paléozoïque, les Permothemistida, les Ephéméroptères et les Protodonates fossiles et, d'autre part, les Ephéméroptères, les Odonates et les Néoptères actuels. L'articulation alaire de tous les ptérygotes est dérivée d'un plan de base ancestral commun qui réunit des structures présentes chez les fossiles. L'articulation des ailes ancestrales était formée d'une bande serrée de plusieurs sclérites articulés sur huit lobes tergaux latéraux et en ligne avec huit paires de nervures alaires. Les sclérites axillaires des Néoptères et les plaques axillaires des Paléoptères sont des sclérites complexes, aboutissements de la fusion de plusieurs sclérites de la bande originelle. Les articulations des Paléoptères et des Néoptères ont évolué différemment et on y observe (*i*) la présence ou l'absence d'un espace au niveau cubital, (*ii*) la présence ou l'absence d'un sclérite complexe, le 3^e Ax, pouvant tourner et pivoter et (*iii*) une composition différente de tous les sclérites complexes. Les adaptations au vol plané et au repliement des ailes le long de la bande articulaire font l'objet d'une discussion. Un nouvelle interprétation, basée sur les structures fossiles, des racines des nervures, des secteurs des nervures et de leur mode de repliement près de la base est proposée. La symétrie sous-jacente des sulcus tergaux thoraciques, des sclérites articulaires et de la nervation alaire semble indiquer l'existence d'une pro-aile presque symétrique sans fonction de vol, mais capable de mouvements vers le haut et vers le bas. Les indices de l'existence d'une articulation dans les ailes larvaires au Paléozoïque et l'évolution de stades métamorphiques ont été examinés. Les lacunes dans les travaux paléoentomologiques font l'objet d'une discussion. Les critères d'établissement des principaux groupes de ptérygotes sont repensés. Il semble que l'aile ait pris son origine dans le premier segment (épicoxa) de la partie supérieure de la patte euarthropodienne et dans son exite. Un podomère épicoxal s'est incorporé à la paroi corporelle et s'est scindé ensuite en un anneau articulaire de sclérites dorsaux et ventraux; un exite épicoxal s'est aplati et est devenu une pro-aile. La pro-aile a fonctionné d'abord sur une rangée de pivots issus de l'épicoxa et de la subcoxa (pleure), puis est devenue mobile grâce à la musculature épicoxale de la patte.

[Traduit par le journal]

Introduction

The development of wing articulation, along with a flightworthy wing blade and the adaptation of certain muscles for flight, are undisputably the structures which brought winged insects into existence and dominance. These three components have developed interdependently and their evolution cannot be considered separately. A credible hypothesis of wing origin must also explain, with equal credibility, the sources of both the articulation and musculature.

It has long been suspected that wing articulation in the Pterygota is misunderstood. Snodgrass (1935), in his textbook dealing with all major aspects of insect morphology, did not attempt a detailed homologization between the paleopterous and neopterous articular sclerites. Hennig (1981) formulated the current situation as follows: "One of the most urgent tasks for future phylogenetic research in entomology is a careful comparative functional–morphological investigation of the basal articulation of the wing in all orders, and it is surprising that no more than the first steps for this have been carried out so far."

Most authors agree with Martynov (1924) that the first split of Pterygota was into Paleoptera and Neoptera. These two major divisions differ from each other in wing articulation and in some characters of wing venation (Kukalová-Peck 1978). The ground plan of musculature was probably inherited by both groups and became modified only after the split, at lesser (ordinal) levels (see Brodskii 1970; Kukalová-Peck 1978; Boudreaux 1979 (for some aspects of musculature); Hennig 1981).

Presently, it is not known how the difference in the wing articulation between Paleoptera and Neoptera came into being, because full homologization of articular sclerites and of wing venation is still wanting. Such homologization, however, is necessary because otherwise there will always be room for the possibility that the articulation may be a "new" structure that is only partially or not at all homologous within all Pterygota. In the recent past, and with greater frequency, either Ephemeroptera (Lemche 1940; Boudreaux 1979), or Odonata (Kristensen 1981) have been classified as closer to Neoptera than to the other paleopterous orders. Some entomologists consider Paleoptera to be a grade and not a natural phylogenetic group (Boudreaux 1979; Rohdendorf and Rasnitsyn 1980; Rasnitsyn 1980; Kristensen 1981; Matsuda 1981). By carrying the set of arguments against homology further, the Pterygota emerge as a diphyletic or still more logically as a triphyletic group, as separate ephemeropteroid, odonatoid, and neopteroid lineages. The ultimate inescapable implication is that insect wings must have originated two or three times. This conclusion was proposed by Lemche (1940), Wille (1960, cited in Hamilton 1971, 1972), Smart (discussion in Wigglesworth et al. 1963), Matsuda (1981), and LaGreca (1980).

The chain of logic described above is contradicted by the fact that the number of shared similarities in wing characters of diverse paleopterous orders, as well as similarities between paleopterous and neopterous wings, increase dramatically in the Paleozoic. The fossil evidence for this is massive (Kukalová-Peck 1978; Hennig 1969, 1981). Also, the evolution of wings and wing articulation was interdependent and therefore the ground plan must be shared by all pterygotes. We should expect that the articulation pattern of modern insects is derived from a common ancestral pattern that is yet to be recognized.

The currently accepted general model of the ground plan of pterygote articulation is based upon wing articular sclerites present in modern Neoptera. The ancestral arrangement is presumed to have consisted dorsally of the first, second, and third axillary sclerite (1Ax, 2Ax, and 3Ax) and ventrally of one or several basalaria and subalaria. In 1978 I tried to interpret the then available articulation of Paleozoic Paleodictyoptera by using the 1Ax–2Ax–3Ax scheme. However, after working with fossil articulation for several more years and finding new excellent material with a completely preserved set of articular sclerites, it became evident to me that the neopterous scheme cannot be used for the Paleoptera.

There is no doubt that all neopterous orders share the 1Ax–2Ax–3Ax original articular model. The characteristic neopterous 3Ax is articulated between the posterior tergum and the cubitoanal part of the wing and provides Neoptera with a wing folding device. By the pull of the attached wing flexor muscle, 3Ax pivots and turns into the anterior membranous "window" and the wing becomes folded backwards over the abdomen and locked securely in the resting position. The 3Ax sclerite and the "window" are apomorphic for Neoptera and are not present in Paleoptera whether they do fold (Diaphanopterodea[1]), or do not fold their wings (Paleodictyoptera, Megasecoptera, Permothemistida (= Archodonata), Ephemeroptera, Protodonata, and Odonata) (Kukalová-Peck 1978). In contrast, the muscle homologous to the wing flexor muscle is plesiomorphic for all Pterygota (Snodgrass 1929, 1935).

In Ephemeroptera, there are two sclerites in a position similar to the neopterous 1Ax and 2Ax, but they are differently set and do not articulate in the same way (Grandi (1947) calls them "pseudopteralia"). The muscle homologous to the wing flexor muscle is inserted at the posterior part of the large axillary plate (Snodgrass 1929, 1935), which is also called the medial or median plate, located centrally at the wing base, instead of onto 3Ax. The axillary plate of Ephemeroptera (Fig. 3) (and Odonata) is a composite cluster of several sclerites which is antero-distal to the position of the neopterous 3Ax (Kukalová 1960; Boudreaux 1979; Hennig 1981).

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[1] Diaphanopterodea are the sister group of Paleodictyoptera, Megasecoptera, and Permothemistida, which did not acquire a gliding ability. They are the most primitive pterygotes known so far (Fig. 1).

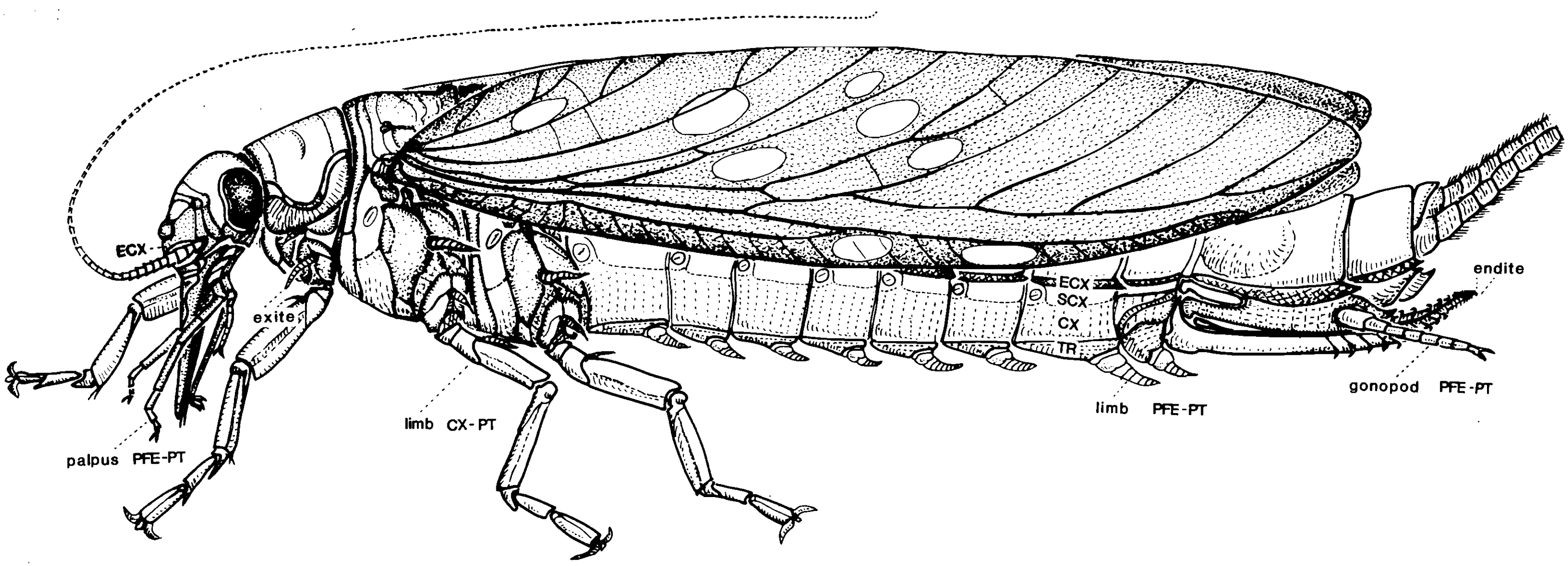


FIG. 1. Appendages and modifications in the most primitive known pterygote order, Diaphanopterodea (Paleoptera, Paleodictyopteroidea). The epicoxa is part of the head capsule under the ocelli and eyes, and forms the articulation around the wings and the keeled lateral lamellae (paranota) in the abdomen. The thoracic pleuron consists of an incorporated subcoxa; the abdominal pleuron consists of a subcoxa, coxa, and trochanter. In the head, the subcoxa, coxa, trochanter, and endites form the mouthparts. Free limbs (palpi) start with the prefemur, all segments including the patella are fully articulated, a basitarsus is present, the tarsus has two subsegments, and the posttarsus carries two claws. The thoracic free limbs start with the coxa, the trochanter and prefemur as well as patella and tibia are separated by deep sutures, the basitarsus is slanted, and the tarsus has primitively only two subsegments. Exites were found on the subcoxa and coxa; the presence of a prefemoral exite is unconfirmed but likely. Thoracic epicoxal exites evolved into wings; abdominal epicoxal exites became appendages of aquatic larvae but became reduced in terrestrial larvae and adults. Abdominal free limbs start with the prefemur: the pregenital limbs are reduced, have only one claw, and were tucked under the body; gonopods were long, fully segmented, and had two claws. This is a martynoviid in sucking position with the labium folded back like a Z and leaning against the spread glossae and paraglossae. The reconstruction was based on observations of over 400 specimens, but was based mainly on beautifully preserved material from Lower Permian strata of the Urals (specimen Nos. 1700/3300, 3303, 3304, 3305, 3308, 483, 485, 488, 490, 494, 495, and 497, Paleontological Institute, Academy of Sciences, U.S.S.R., Moscow. Leg modifications, with exclusion of the epicoxa, were done in cooperation with E. L. Smith; extensive comparisons with modern insect dissections and other arthropods will be given in his forthcoming book. For all abbreviations in the figures, consult the list given at the end of this paper.

In addition to sclerites participating in the composite axillary plate and the "1Ax" and "2Ax," well sclerotized primitive Ephemeroptera have several more sclerites in the anterior and posterior parts of the articular area (Tsui and Peters 1972) that are not found in the Neoptera. These sclerites become better visible if a well-sclerotized siphlonurid is lightly stained with fuchsin and then observed as it dries out; this makes the desclerotized areas visible.

The articulation of the Odonata is highly autapomorphic and was influenced by a secondary switch to flight powered almost entirely by direct musculature (Boudreaux 1979; Hennig 1981). In the anterior part of the articular region where large Ephemeroptera have "additional" sclerites and Neoptera mostly lack sclerites, Odonata have an "additional" large and well-sclerotized composite sclerite (Neville 1960), called (by typology) the "proximal humeral plate." The axillary plate of Odonata, located centrally at the wing base, looks similar to that of Ephemeroptera, but sclerites between this and the tergum are quite different in arrangement and number (Tannert 1958; Tsui and Peters 1972). There are no sclerites of the neopterous type and articular position (Matsuda 1970, p. 390; see Hamilton 1971, Figs. 13–16, for an opposite interpretation).

The data reviewed above lead to two alternative conclusions: either (*i*) we presume, along with Matsuda (1981), that the wing articulation and the wing itself originated twice or three times; or (*ii*) that the ground-plan model of pterygote articulation based upon neopterous articulation is erroneous.

Fossils as clues for an all pterygote wing articulation ground plan

Attempts to improve homologization of wing articulation and venation are not new to this paper; a long list of proposed changes by different authors has been reviewed and discussed by Matsuda (1970), Hamilton (1971, 1972), Boudreaux (1979), and Brodskyi (1979). More recently, Kukalová (1960), Kukalová-Peck (1978), Brodskyi (1979), Boudreaux (1979), and Hennig (1981) expressed belief that Paleozoic fossils contain clues for homologization by preserving evolutionary states closer to the ancestral ground plan. While certain advancements in understanding have been achieved, the new data introduced in this paper show that only a radically different approach would make homologization possible between articulation and venation of Ephemeroptera, Odonata, and Neoptera.

In 1981 I was invited to the Field Museum, Chicago, which has an outstanding collection of Middle Upper Carboniferous (Westphalian C-D) insects from Mazon Creek, Illinois, a vast area of spoil banks resulting from coal mining (Nitecki 1979). The collection was assembled with the substantial help of devoted volunteers and private collectors under the auspices of Field Museum paleontologist Dr. E. S. Richardson, Jr. A crucial breakthrough in the search for the articulation ground plan of pterygotes came from a giant paleodictyopterid *Mazonopterum wolfforum* Kukalová-Peck and Richardson, 1983, belonging to the most primitive paleodictyopterid family Homoiopteridae. The specimen is owned by Mr. K. Daggett, Chicago. By a stroke of luck, this homoiopterid, which has a wing span of 37 cm, was preserved in a perfectly outstretched position with exposed articulation. The specimen was large enough to have all dorsal articular sclerites well sclerotized, and a complete and undamaged set was carefully prepared from the counterimprint of the right wing (Kukalová-Peck and Richardson 1983, Figs. 3, 4, 5, 6, 9, 11).

The full, completely preserved articulation of homoiopterid Paleodictyoptera consists of a band of numerous sclerites which are aligned with veinal pairs, presumably to keep the blood canals open. In a study now in preparation, the homoiopterid articulation is homologized with that of Paleozoic Diaphanopterodea, Protodonata, modern Odonata, Permothemistida, Ephemeroptera, and with the partially desclerotized articulation of modern Ephemeroptera. Lastly, homoiopterids are compared with modern primitive Neoptera (articulation of Paleozoic Neoptera has not yet been found in a suitable state of preservation). Since the documentary material is quite extensive, the discussion must continue in a set of subsequent publications. Here, only brief comparisons can be given.

Comparative study has shown that if a large number of articular sclerites are considered as the original state, and the clustering of these sclerites into apomorphic composites is accepted as the main evolutionary trait, then *all* "odd" sclerites between the paleopterous orders and the Neoptera can be homologized. It appears that previous difficulties were caused by "forcing" a derived neopterous articular pattern upon the more plesiomorphic, less derived paleopterous pattern.

A new wing articulation theory cannot be proposed or even discussed without considering also the origin of wings, the possible wing homologue, flight musculature, nymphal wing development, metamorphosis and, ultimately, the state of the ancestral euarthropodan leg. The present paper is concerned with these problems.

Any new articulation hypothesis must consistently explain the multiple and extremely varied data accumulated through many years by students of entomology. I believe that my interpretation of the fossil record is basically correct and hope that it will stimulate further investigation. However, the subject is very complicated and concerns not only several entomological disciplines, but also arthropods in general. So far, I have had to restrict my contribution mostly to the comparative outer morphology of Paleozoic and modern insects. It is therefore possible that with more exact methods some of the sclerite homologues proposed in this paper or in the future will be found to be faulty. Whatever the adjustments would be, they should not change the fact that the paleopteran and neopteran wing articulation evolved from a common band of numerous adjacent sclerites that are found in the fossils and diverged in two different ways. The phylogenetic implication is that Paleoptera are not a "grade," as is sometimes suggested, but a valid phylogenetic unit equivalent to Neoptera.

Pleural origin of wings

The most diverse animals are winged insects, containing some 75% of known animal species. The adaptive success stemming from insect wings has long been recognized, but the question of their origin has not yet been satisfactorily answered. In a previous paper (1978) I showed that fossil and other evidence narrows down the choice of feasible hypotheses on wing origin. The possibility that wings evolved from solid, immobile, lateral extensions of the terga (the paranotal theory of wing origin) was rejected. Wings were suggested to be pleural appendages and to be primitively serial, occurring on three thoracic segments as wings and on nine abdominal segments as winglets. All wings were primitively movable and articulated in both nymphs and adults. Gliding and soaring were identified as secondary adaptations that occurred many times in members of diverse pterygote groups. The postembryonic development of nymphal wings was documented as gradual, but only as long as nymphal wings were articulated. After the wings became immobilized and fused with the tergum (for streamlining), the metamorphic instar occurred. The original function of the metamorphic instar was seen as *restoring wings* to a condition with articulation, larger size, and function. It was claimed that the metamorphic instar occurred in some groups before the start of the fossil record, but in others during documented periods, in Late Carboniferous, Permian, and in Early Triassic. Consequently, metamorphosis originated in parallel in several lineages and is polyphyletic.

One major question was not answered: What is the identity of the wing precursor?

Ontogenetic evidence

Fossil evidence focused attention on previously little-noticed supporting data in modern ontogeny that wing buds in primitive insects occur in the pleural wall (Tower 1903; Bocharova-Messner 1959, 1965, 1968, 1971). Alar thermoregulation has been examined as a possible function of the articulated pro-wing (Douglas 1981).

Physiological evidence

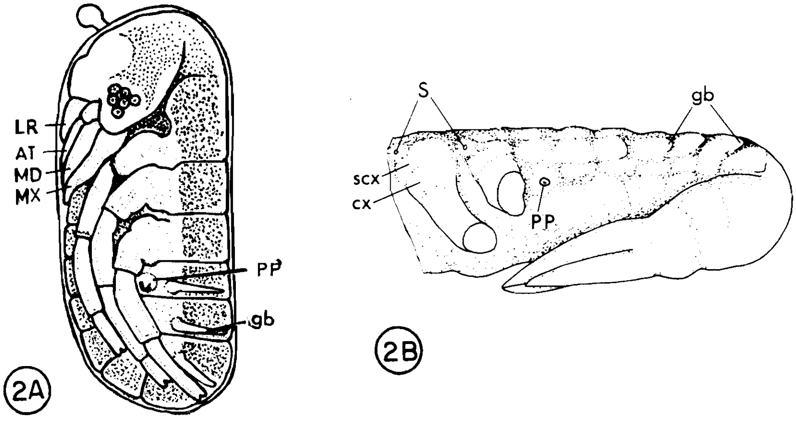
The pleural appendage theory of wing origin recently found significant support from investigations into the neural control of locust flight. Interneurons firing flight impulses are also present in the first three abdominal segments (Robertson *et al.* 1982). These neural structures are residual and can be explained by the previous existence of movable, serial abdominal wing homologues, but not by the paranotal theory. Were the primitively immobile, lateral tergal outgrowths serially homologous with thoracic wings, as anticipated by the paranotal theory, the flight promoting interneurons would not occur in the abdomen of any modern insects.

Embryological evidence

Important contributions to the knowledge of pleural appendages in the embryos of Megaloptera, Trichoptera, and Mecoptera have been offered by Ando (1970), Ando and Haga (1974), and Miyakawa (1979). Pleuropodia are embryonic or temporary larval modifications of the limb buds that occur on the first abdominal segment in many insects. A temporary series of pleuropodia – abdominal legs – gonopods also exists in the embryo of Mantodea (Görg 1959, in Matsuda 1976, p. 187), and in other insects. According to Miyakawa (1979), a megalopteran embryo develops pleuropodia and seven pairs of serial (leg) swellings and, above them, eight pairs of tracheal filaments (Fig. 2A). Filaments are born posterolaterally from spiracles, i.e., in the position of wings, and are clearly pleural. Simultaneous occurrence of leg-derived pleuropodia and tracheal filaments shows that they cannot be legs shifted dorsally as often believed (Kukalová-Peck 1978). They are homologous to tracheal gills of mayflies and, as interpreted in this paper, represent abdominal exites. Pleuropodia and tracheal filaments also occur simultaneously in the nymphs of primitive Plecoptera and Zygoptera (Fig. 2B, Euphaeidae and Polythoridae) (Norling 1982), in which filaments sometimes show residual annulation characteristic for the leg exites of Paleozoic Pterygota and modern Crustacea.

In modern Mecoptera, there is yet another series of appendages besides legs and wings. In the embryo of *Panorpa pryeri* (Ando and Haga 1974) eight pairs of styliform appendages occur; these are not homologous with thoracic legs (or pleuropodia), because they are located more ventrally.

The set of three plesiomorphic pleural appendages found in the embryos by Japanese entomologists appears to be serially homologous with these present in the genital segments, i.e., of older mayfly nymphs (in the Paleozoic), as schematically summed in Fig. 4 and represent wing series, leg series, and endite series. The



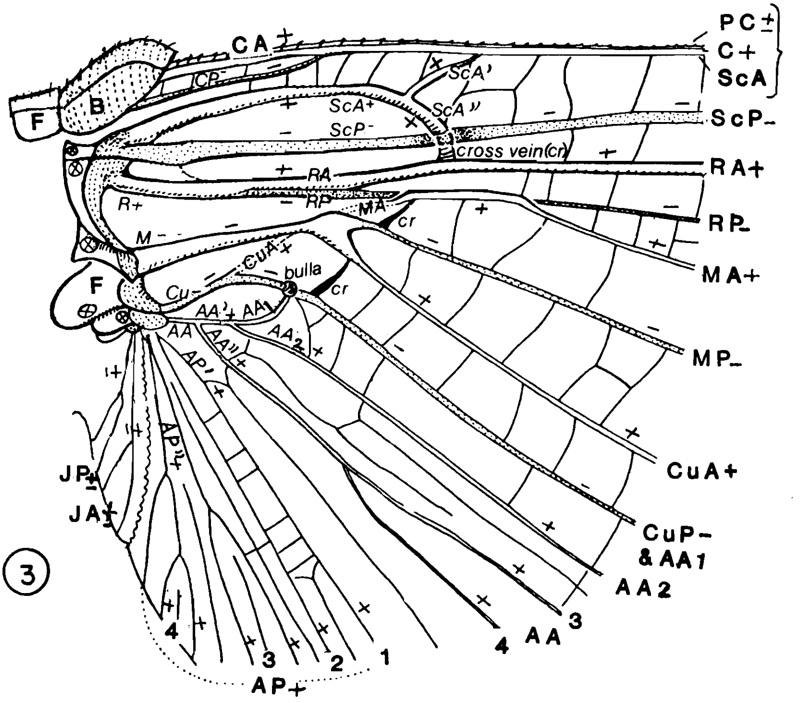


FIG. 2. (A) Embryo of *Protohermes grandis* (Megaloptera) in the 9th day of development, lateral view. Pleuropodia (PP), which are derived from legs, occur on the same segment but much lower than a series of tracheal gills (*gb*) and therefore cannot be mutually homologous. Gills evaginate at the same level and posteriorly from spiracles, as do wings. Terga in the head and trunk (stippled) agree with the interpretation shown in Fig. 1. After Miyakawa 1979. (B) Embryo of *Epallage fatime* (Odonata, Zygoptera) showing identical position of pleuropodia ventrally from the segmental gill buds. After Norling 1982. FIG. 3. Paleozoic Protereismatidae (Ephemeroptera), base of the wing with eight basivenalia (B) and eight fulcalaria (F). All sclerites are primitively delimited by distinct sutures. Subcostal through jugal fulcalaria carry a series of muscle scars (⊗). Precostal and costal veins are not fused but adjacent. Note plesiomorphic serrate PC, branched CP−, branched ScA+, RP below the superimposed RA, and two branched jugal veins. Numerous braces are formed by CP−, ScA′ and ScA″, MA, CuA, and supplementary braces by cross veins (*cr*). The complicated anal brace is formed by AA and AA′ and AA'_1 and is prolonged by a cross vein brace. A similar pattern of veinal fusions and the anal brace, all arranged in parallel sections, is built into the venation of Odonatoidea. *Protereisma* sp., hind wing. Cumulative drawing based upon 25 wings with articulation (Peabody Museum, Yale University), and on specimen nos. 3419 and 3411 (Museum of Comparative Zoology, Harvard University) from Lower Permian strata of Kansas. After Kukalová-Peck in Hubbard and Kukalová-Peck 1980, Fig. 2; improved reconstruction of the original.

ventral series generating "prolegs" is in the position of vesicles, gonapophyses-parameres, or penes, which in turn originated from euarthropodan endites (partly Boudreaux 1979; E. L. Smith, personal communication). Therefore, larval prolegs are very probably derived from the euarthropodan leg endites (in contradiction to Hinton (1955), who suggested multiple, secondary origin of the "prolegs"; and in contradiction to Matsuda (1976), who interpreted "prolegs" as homologous to the thoracic legs).

Developmental genetics evidence

In the last decade, extensive genetic work has been done with clones, polyclones, and compartments of *Drosophila*, especially on wing discs (Garcia-Bellido 1975; Crick and Lawrence 1975; Lawrence and Morata 1976; Morata and Lawrence 1977; Garcia-Bellido 1977; and the compilation by Garcia-Bellido *et al.* 1979). The results of earlier genetic studies were considered as potentionally contradictory to the hypotheses deriving the insect wing from a pleural appendage (Matsuda 1981). However, according to the geneticists cited above, just the opposite is true. In the developmental sequence of *Drosophila*, the wing disc separates from the leg disc, not from the tergum, as follows.

At the very early stage in the embryo the body is divided into "compartments." The mesothoracic segment arises from two neighbouring compartments. Soon after this polyclones of the adult wing are separated from polyclones of the adult leg. Still later and within the already developing wing, the wings become subdivided into the dorsal and the ventral part (Garcia-Bellido *et al.* 1979, p. 105).

Another important observation supports the new thesis on wing articulation introduced in this paper: that the articulation is not tergal but evolved from the first leg segment of the euarthropodan leg (called here the epicoxa), which became incorporated into the body wall above the pleuron (subcoxa). The event is echoed in the wing disc of *Drosophila* as follows:

The left wing disc, inside the larva, produces the left wing of the insect and that part of the dorsal left side of the thorax next to the wing (Crick and Lawrence 1975, p. 340; Garcia-Bellido *et al.* 1979).

Still another observation suggests that the wing is a lobelike, collapsed, and secondarily flattened appendage (of the leg) in the following way. During metamorphosis, the wing is first formed as a bag with a single layer of epithelial cells. The bag then collapses and folds to form the adult wing consisting of a double layer of epithelial cells (Crick and Lawrence 1975, p. 340.)

The above-cited data are consistent with the new hypothesis of wing origin proposed in this paper, which interprets insect wing as pleural and an appendage of the first leg segment (specifically, the epicoxal exite), and wing articulation, as the incorporated but fragmented epicoxa.

Another interesting problem are the homoeotic mutations of *Drosophila*, which are sometimes considered as "monstrous," having little or no relationship to the evolutionary morphology of the organism. It seems that the homoeotic mutations make evolutionary sense. For instance, the mutation *Antennapedia*, which changes an antenna into a leg, is a serial gene substitute of a homologous organ, because the insect antenna evolved from a leg (Boudreaux 1979). Another mutation transforms part of the eye into wing tissue. This seemingly completely unrelated exchange of genes may also be a serial gene substitution, according to the new wing articulation hypothesis introduced here. The thoracic (dorsal and ventral) wing articulation is considered to be serially homologous to the part of the head capsule just below the eye, and the eye (and ocelli) are interpreted as being primitively located between the cephalic tergum and the first euarthropodan leg segment (epicoxa) (Fig. 1).

Tissue transplant evidence

Another support to the new thesis of the alar (i.e., pleural) origin of wing articulation came from transplantation of the wing discs of *Lymantria dispar* (Lepidoptera) to the tergum (Stenzhorn 1974). The wing anlage produced not only the wing, but also the so-called tegula, axillary sclerites, and most notal wing processes, all interpreted here as parts of the primitive articular band that was derived from the upper leg.

Alternative interpretations

The pleural origin of wings has been recently accepted by a growing number of entomologists, but a variety of modifications and critiques have been offered.

Wootton (1981*a*) virtually adopted the pleural origin of wings, but cautioned that fossil evidence for primitive articulation of nymphal wings is unconvincing. Wootton must have overlooked the fact that Sharov (1957*a*, 1957*b*, 1960, 1966), Kukalová-Peck (1978, p. 61) and Carpenter (1979, p. 270) have together mentioned more than 500 detached juvenile wings, of representatives of both paleopterous and neopterous orders, from Upper Carboniferous and Permian deposits. These wings are all separated from the body in the same way as adult wings that break off at a region of weakness in the articulation. Modern nymphal wings only rarely separate from the terga because they are not articulated, but fused.

Rasnitsyn (1981, p. 332) agreed that wings are pleural, confirmed that some Paleozoic nymphs have articulated wings, and regarded the wings to be homologous to subcoxal exites[2]. But he interpreted the course of wing evolution through a modified paranotal theory, as follows. The pro-wings migrated upward, became fused with the terga into complex paranota, and then were used for gliding. Through gliding, the wings again became loosened from the terga by the mechanisms envisioned in the paranotal theory.

Rasnitsyn's modification combines events which are difficult to explain. (*i*) The migration of the subcoxal exite from its primitive position in the intersegmental membrane ventrally from the subcoxa, through the whole segment, to a new position in the membrane dorsally above the subcoxa is highly unlikely. (*ii*) Since the modern arthropod leg exites either lack musculature or have muscles only basally (Norling 1982), but the wing-exite is moved by the combined intrinsic and extrinsic leg-segment type of musculature, where did the muscles come from if the subcoxal exite migrated away from its segment? (*iii*) How could the intricate musculature and articular sclerites rocking the wing base have evolved if gliding requires neither articulation nor rocking movement? (*iv*) How did the flight-promoting interneurons occur in the abdomen of living locusts if the pro-wings were fused with the terga?

Matsuda (1981) also accepted the pleural origin of the wing, but failed to consider massive evidence of shared characters in the fossil record supporting a monophyletic origin of wings (Kukalová-Peck 1978). He claimed that insect wings are diphyletic (at least) and that odonates, because they have different venation and articulation, supposedly evolved their wings separately from all other pterygotes.

However, the prevalent interpretation of odonatan venation with two missing sectors (MP and CuA) is faulty (Riek 1970, p. 173, Fig. 8.2) and it disagrees with the fossil record. Odonatoids have two stems of radial sectors[3] adjacent basally, stems of M and Cu fused basally, a short fusion between MA and RP, and between CuP and AA. Some of these veinal features are present in the homoiopterid Paleodictyoptera (described by Kukalová-Peck and Richardson 1983). Incompletely fused radial stems and all fusions between veins mentioned above are present in Paleozoic Ephemeroptera (Fig. 3). The evolution of the odonatoid venation from an ephemeroid to the odonatoid type is best documented in the oldest known, yet undescribed dragonflies from the Namurian of Argentina (currently in preparation by E. F. Riek (personal communication)). Odonatoid venation has evolved only one step further from an ancient, ephemeroid type of venation as an autapomorphy. Paleozoic Protodonata show a complete, fully homologous pterygote veinal pattern. Recent odonates have an inconspicuous distal part of CuP− which is, nevertheless, present. The odonatan articulation is also neither exceptional nor unique. It only seems to be peculiar, if the neopteran axillaria, which were selected for a completely different type of flight, are used as a model. It will be shown (Figs. 16B, 16E) that odonatan articulation can be derived from a primitive articular band ancestral to all Paleoptera by employing the same evolutionary principles as for Paleodictyoptera, Diaphanopterodea, Permothemistida, and Paleozoic Ephemeroptera (Figs. 16C, 16F).

Pivotal to the interpretation of pleural wings is the composition of the generalized arthropodan leg, especially its upper part, which is still not well known. This fact adversely affects an accurate comparison of the wing and wing articulation with the other arthropods; virtually a dozen seemingly well-reasoned opinions exist to support ideas that are quite diverse (Boudreaux 1979). By far the most detailed morphological correlation between the structure of insects and that of all significant arthropodan groups (based on almost a thousand comparative dissections), was recently finished by E. L. Smith (California Academy of Sciences, San Francisco). It will be published as a morphological atlas (in preparation) and will include the morphological features and some intepretations of fossils contributed by me. The atlas will present much new evolutionary morphological data, some of which are being documented in this paper. However, there is a major dilemma: the fossil documentation is lengthy and must be published separately, in steps. But it was interpreted with a "panarthropodan" viewpoint, i.e., with knowledge of new data discovered by Smith, which can be introduced only in his published atlas. Under the circumstances, it seems reasonable to use Smith's data in interpreting Paleozoic insects by referring to them summarily as "E. L. Smith, personal communication," and to expect that his detailed and extensive correlative study will appear in due course.

Working with fossils

Outline drawings of fossil specimens routinely used for alpha-level taxonomy of fossil insects are of limited use in evolutionary morphology. Only a detailed study of a particular Paleozoic structure, preferably on all available material in one order, homologized with well-preserved material in other Paleozoic orders, and

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[2] The theory that wings originated from leg exites ("stylus theory") was first developed by Wigglesworth (1973).

[3] According to the fossil record (Kukalová-Peck 1978), all wing veins occurred originally as a pair of sectors (primitively + and −) starting from one basivenale. Modern Odonata retained the two-sectors character of the radius vein as a plesiomorphy.

then compared with homologous structures or their vestiges available in Recent insects, is meaningful.

Such integration of morphology does not come easily or quickly, because of shortcomings in the fossil record. The study of a specimen requires, on the average, 3 months or more. Detailed composites may take years to reconstruct, and an extensive parallel comparative study of living material is absolutely necessary. A frustrating factor is that observations are sometimes difficult to share with others if one is unable to personally point out features of a specimen under the microscope. Care notwithstanding, mistakes in interpreting paleontological evidence are bound to occur, but can be corrected as new material and evidence is discovered. Eventually, the morphological record of insect history will become stabilized, as in other well-recorded groups such as mammals, for instance. I apologize here for several changes in interpretation from some of my previous papers. Nevertheless and in spite of the shortcomings, the fossil record provides direct tests of evolutionary conclusions. There is good reason to believe that fossil evidence will ultimately prove to be as beneficial for understanding insect evolution as it now is for vertebrates.

The state of preservation of fossil insects plays an important and often adverse role in interpreting insect articular sclerites. When a rock is split open, the specimen usually separates into an imprint and counterimprint (obverse and reverse) along the plane of maximum weakness. This plane often runs through the body cavity, rather than between the body surface and the rock. Typically, the split is irregular and shows several different layers, all or most of which lie *inside the body*. This type of preservation affects sclerites because they tend to be "scalped" and lifted from the imprint (Kukalová-Peck and Richardson 1983, Figs. 3, 6). The imprint may then show no sclerites, it is as if they had never been present, since they stay embedded in the rock. This secondary state can be misinterpreted as primary morphology (Wootton 1981*a*, p. 338: "the pads of *Rochdalia parkeri* show no convincing sign of articulation"); compare scalped *Rochdalia parkeri*, Wootton 1972 (his Fig. 1), and unscalped *Paimbia fenestrata* (his Figs. 32, 33) and left and right wing articulation in Kukalová-Peck and Richardson (1983, Figs. 3, 6). Disregard for the vagaries of preservation made Wootton (1981*a*) criticize, quite unjustly, my reconstructions of paleodictyopterid nymphs and my "rash conclusion" that pterygote nymphal wings were primitively mobile. Mobility of nymphal wings is richly documented, is now beyond doubt, and has been accepted by specialists for more than a decade. A short review of available data is given in the section "Articulation in early pterygote nymphal wings."

During fossilization, an insect's body is often crushed, creased, crumpled, and scalped and its structures are caved in, compressed, and superimposed. False "sutrues" might result and the specimen might become completely unintelligible. Muscle scars, which would normally be invisible, may occur where the fossil cuticle splits off.

Without considerable experience, an entomologist cannot expect to recognize all features on a complicated fossil, just as a radiologist or embryologist requires training in observation. Also, if perception is marginally difficult, some people lack the patience to discern features. Thus, confirmation of observed facts is sometimes not easy. Fortunately, an evolutionary interpretation based on the study of fossils can almost always be verified when a fossil structure is echoed in some way in a modern representative. If it is not, there is a good chance that the fossilized structure was misunderstood. It might be difficult for a later author to retract the minute, disfigured articular sclerites scattered through the many Paleozoic fossils upon which I have built up, through the years, the new articulation hypothesis. However, raw paleontological data are by far not the only criteria required for an accurate interpretation. If, and only if, the hypothesis does explain coherently and consistently *all* respective data and phenomena in modern entomological disciplines concerning articulation, will it be confirmed and accepted.

Ground plan of the insect leg

I hypothesize here that originally there was an additional segment in the ancestral arthropodan leg, articulated above the subcoxa, and propose for it the name *epicoxa*. In the Pterygota, the epicoxa (ECX) became embedded in the pleural body wall, in the same way as the subcoxa, and became tagmatized (Fig. 4). The thoracic epicoxa broke into multiple sclerites that originally formed an incomplete ring around the prowing, interrupted ventrally by the ventral wing process (VWP) protruding from the subcoxa. The primitive subcoxa (SCX) was large because the thorax was high in order to accommodate the musculature (Fig. 1) and was possibly subdivided by a sulcus. The coxa (CX) was comparatively large and was subdivided by a sulcus. The trochanter (TR) was relatively very short, followed by a longer prefemur (PFE). Legs of Paleodictyopteroidea probably always had a well-developed prefemur (second trochanter), separated by a deep suture from the trochanter. Compared with this, almost all Recent Pterygota, with the exception of odonate nymphs (Snodgrass 1935, Fig. 109), have a fused trochanteroprefemur in the thoracic legs. The subcoxa, coxa, and prefemur primitively bore exites (Figs. 1, 8–12). The femora (FE) of large Paleoptera often carried a proximal swelling (femoral "head"). There was a patella (PAT) separated by an oblique suture from the tibia (TI)

(Kukalová-Peck 1969, 1970*a*, 1970*b*). The tarsus, according to comparative dissections by E. L. Smith (personal communication) is not one subdivided segment, but two segments: a single basitarsus (BT) and a tarsus (T) that originally has probably two subsegments and the posttarsus (PT) (ungues). For an emended diagram of the *Monsteropterum moravicum* leg, see Figs. 8–10.

In the thoracic leg, there are altogether 11 primary segments: 2 segments are embedded in the body wall and 9 compose the free limb. Of these, the tarsus is divided into two subsegments in primitive Diaphanopterodea (Fig. 1) and into four in specialized Permian Diaphanopterodea and in Paleodictyoptera. An identical ground plan as in primitive Diaphanopterodea is probably present in the legs of Monura (Fig. 5). In modern Ectognatha the leg plan is obscured by fusions (Fig. 7), but very likely was identical originally. In Paleozoic Diplopoda the legs do not have a subdivided tarsus but otherwise seem to agree with Pterygota (Fig. 6).

There is strong evidence, fossil and otherwise, that reduced (tagmatized) abdominal legs are plesiomorphic for all Insecta, Entognatha, and Ectognatha. Free abdominal legs occur in Diplura (seven pairs, all starting with a prefemur, Fig. 7), Protura (three pairs) and Collembolla (one pair) (Boudreaux 1979). In modern Archeognatha (Machilidae) abdominal legs, called somewhat imprecisely "styli," are present on segments II to IX (Smith 1970). In Dicondylia, primitive Thysanura have legs on segments II to IX, and pterygote embrya, on segments I to X (Matsuda 1976) but in modern larvae and adult Pterygota, free pregenital legs have disappeared. Only gonopods occur in some primitive orders (Smith 1970; Boudreaux 1979), and the leg appendages (endites) form the primary genitalia in both sexes (E. L. Smith, in preparation).

As is to be expected, the presence of abdominal legs in Paleozoic insects is much more pronounced and, as an especially important aspect, the legs provide landmarks for the interpretation of the abdominal pleuron and of genitalia. According to my observations, the full series of nine abdominal legs was found, so far, in the following pterygote orders: adult Diaphanopterodea (Fig. 1) and Permothemistida and some juvenile Ephemeroptera; some aquatic nymphs of Neoptera (Kukalová-Peck 1978, Fig. 35) also have nine pairs of abdominal winglets. Free gonopods of both sexes ending with ungues (claws) have been found so far in Diaphanopterodea (Fig. 1) and in Ephemeroptera. The primitive epicoxa is often keeled; according to my joint study with E. L. Smith, the subcoxa, coxa, and trochanter of the pterygote abdomen are fused into one plate (Fig. 1), the abdominal pleuron (in contrast, the thoracic pleuron is formed only by the subcoxa). Rarely, faint sutures occur in fossils between the subcoxal, coxal, and trochanteral plates, specifically in a protodonate nymph No. PE 30272 from Upper Carboniferous strata of Illinois, Field Museum, Chicago (Figs. 30A, 30B), and in segments of Diaphanopterodea from Lower Permian strata of the Urals, U.S.S.R. (Paleontological Institute, Academy of Sciences U.S.S.R., Moscow) (Fig. 1). Abdominal legs, genital segments, and genitalia will be documented in a later publication.

The pregenital free legs in fossils are alway segmented, but not fully, because they are rudimentary. Exceptions are legs of abdominal segment VIII in a male ephemerid (No. 4374 from the Lower Permian strata of Kansas, Museum of Comparative Zoology, Cambridge), which are short but fully segmented and end in claws, so that this specimen has two pairs of claspers with ungues. All the data introduced above are from work in preparation and have been integrated with the research on modern insects conducted by E. L. Smith (personal communication; detailed discussions will be presented in his forthcoming book). The data are mentioned here for the integrity of the fossil record in comparing the thoracic and abdominal upper leg, namely the epicoxa and pleuron (Figs. 1, 4). The free leg of primitive male claspers and female gonopods (Fig. 1) in fossils is fully segmented, starts with the prefemur, and ends with a posttarsus (claws). By serial homology, the pregenital rudimentary legs also start with a prefemur, a presumption which agrees with the presence of delimited subcoxal, coxal, and trochanteral plates in the pleuron of Protodonata (Figs. 30A, 30B) and Diaphanopterodea (Fig. 1), and of claspers VIII in Epheroptera (mentioned earlier). The Diplura (Fig. 7) have an identical composition of the thoracic and abdominal wall reinforcement as do the Pterygota, even if the similarity is somewhat obscured by the fact that the subcoxa is desclerotized and subdivided, and the coxotrochanteral abdominal plate is fused with the sternum. Note that the rudimentary two-segmented free abdominal limb starts with the prefemur, as does that of fossil pterygotes.

In the primitive pterygote head, the epicoxa probably forms the part of the head capsule immediately under the ocelli and the eyes (Kukalová-Peck 1983), while the free head appendages start with the subcoxa (E. L. Smith, personal communication). One homoeotic mutation in *Drosophila* transforms part of the eye into wing tissue (Garcia-Bellido *et al.* 1979), which lends support to this interpretation.

In Paleozoic Pterygota, exites on the upper leg were probably quite common, but they are only rarely recognizable in fossils. Not only are the exites thin walled, but they also blend inconspicuously with the uneven matrix. An interesting feature of Pterygote exites is the annulation, since in Crustacea the exites are also primitively annulated (Figs. 8–12). Almost certainly, precoxal, coxal, and prefemoral exites are present in thoracic legs of all or almost all Diaphanopterodea, Paleodictyoptera (Figs. 1, 8–12), and Ephemeroptera (Figs. 11, 12); very likely, additional occurrences in other orders will be reported in the future. Thus there is evidenced that insect legs were primitively polyramous, like those of primitive arthropods, and not uniramous, as espoused by Manton (1977, and references therein) and some other arthropodologists.

It is presumed here that the epicoxa surrounded the wing dorsally, ventrally, and laterally, as an incomplete ring. The epicoxal ring changed into the dorsal and ventral wing articulation (pteralia; basalaria and subalaria). The centre of the insect wing base is at the bottom of the (epicoxal) segment, and above the next (subcoxal) segments inflexion, i.e., at the original site of leg exites in Arthropoda. Because of this position, the wing precursor is likely to have been the epicoxal exite.

Insect leg exites as wings

In the previous discussion it has been suggested that the insect wings originated from euarthropodan exites. The most notable reason for this interpretation is the position of the wing, in the membrane between two (embedded) leg segments, the epicoxa and subcoxa. Original euarthropodan exites are also born between segments and are lobelike evaginations of the membrane, commonly found on the legs of modern Crustacea. In the aquatic forms, exites of the upper leg are respiratory (Boudreaux 1979). In the primitive crustacean *Anaspides*[4] respiratory exites are flat and leaflike, similar to wings in shape. In terrestrial arthropods respiratory exites are usually suppressed, because they are most useful only in an aquatic environment.

In modern Archeognatha (Machilidae) amuscular coxal exites are present usually on the second and third

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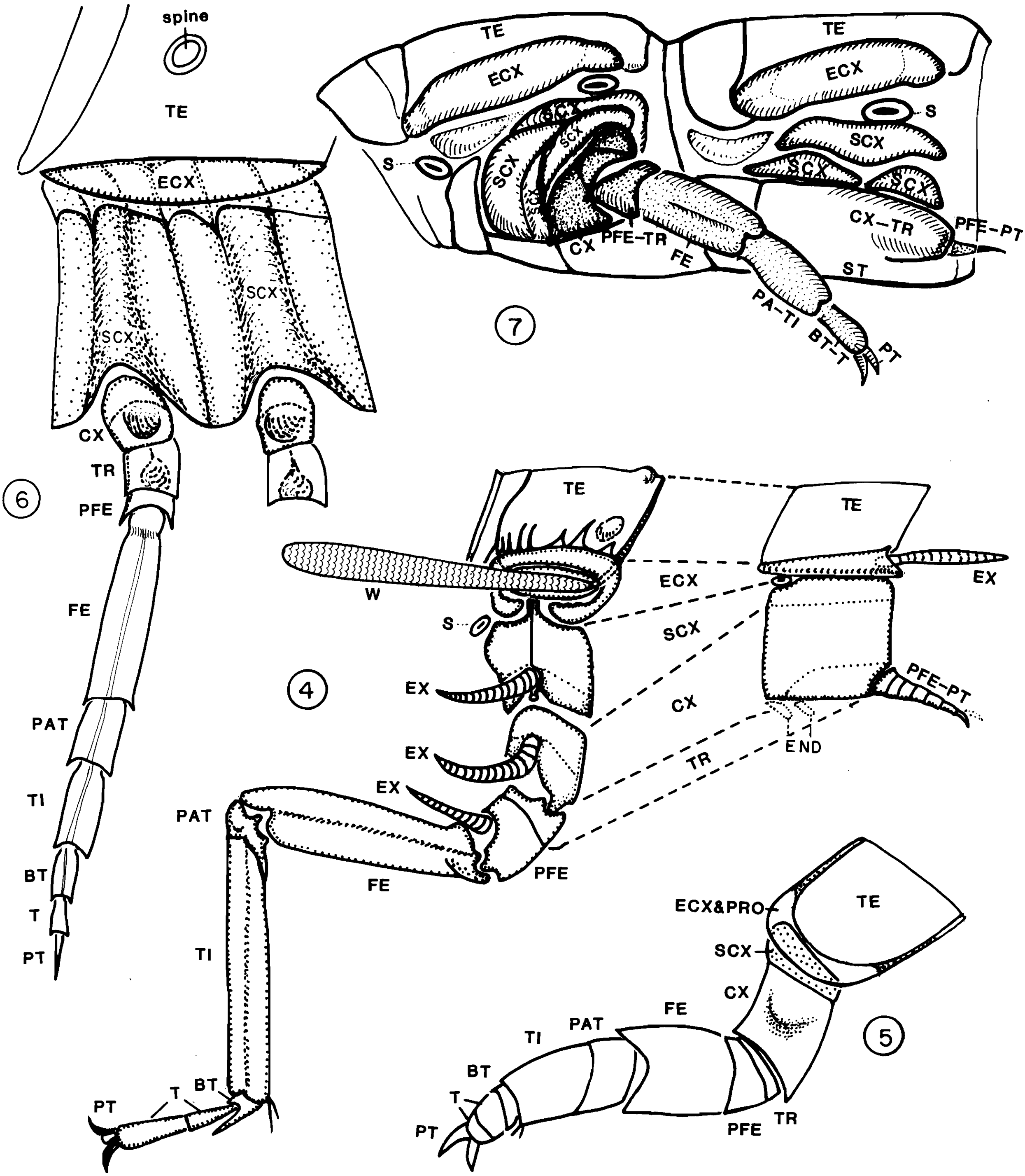
[4] Hennig (1981) correctly recognized coxal appendages in Archeognatha as exites, but erroneously homologized respiratory exites of the primitive crustacean *Anaspides* with the vesicles of Archeognatha. Vesicles are euarthropodan endites and are serially homologous with gonapophyses and with parameres (Štys 1959; Boudreaux 1979), and with penes (E. L. Smith, personal communication).

FIG. 4. Model of the original pterygote leg in the thoracic and abdominal tagma. The thoracic wing rests centrally on the subcoxa in the position of an euarthropodan exite and is surrounded dorsally and ventrally by an epicoxa turned into articulation. The abdominal exite is articulated under the epicoxa, shifted more or less posteriorly, and is moved by leg musculature. The thoracic pleuron is formed by an incorporated subcoxa and the abdominal pleuron by a subcoxo-coxo-trochanteral plate. Coxal and trochanteral endites are used mainly in genitalia and in mouthparts. The free limb starts with the coxa in the thorax and with the prefemur in the abdomen, as in Diplura (Fig. 7). The basitarsus (BT) has a separate muscle insertion and was recognized as an euarthropodan podomere by E. L. Smith. Claws were primitively present in palps and thoracic and abdominal limbs. They then became reduced in pregenital abdominal limbs, but were preserved until the end of the Paleozoic in palps and gonopods of Paleoptera and some Neoptera. FIG. 5. Monura (Thysanuroidea), mesothoracic leg. Epicoxa and pro-wing fused together into a lobe (ECX&PRO); subcoxa (SCX) relatively short and well sclerotized; coxa (CX) much shorter than typical coxa of modern Thysanura and with bulging area where coxal adductor is inserted; trochanter very short, fused with a relatively long prefemur; large patella well separated from tibia by suture; basitarsus short and typically slanted; tarsus with two subsegments and pretarsus probably with two ungues (instead of one as anticipated by Sharov 1966). *Dasyleptus* sp., specimen No. P11E 751, collection of C. Cozart, Chicago, from Upper Carboniferous strata of Mazon Creek, Illinois. Original drawing. FIG. 6. Myriapoda, Paleozoic Diplopoda, primitive diplosomite with keeled epicoxa and fully embedded, well sclerotized subcoxa. The number of leg segments is the same as in insects but the patella is fully articulated and the tarsus is not subsegmented. Composite scheme based on *Acantherpestes major*, specimen No. PE 25432, Field Museum, Chicago, from Upper Carboniferous strata (Westphalian) of Illinois, and *Acantherpestes vicinus*, from Upper Carboniferous strata of Central Bohemia (photograph by Kraus 1974, Fig. 2). FIG. 7. Insecta, Endognatha, Diplura, the largest modern japygid; metathorax and first abdominal segment. Subcoxa is embedded in the body wall, desclerotized into several separate bulges, and expressed differently in thorax and abdomen. Trochantero-prefemur and patello-tibia in thoracic legs fused as in ectognaths. In the abdomen the epicoxa through trochanter are incorporated in the body wall, and the free limb starts with a prefemur as in pterygotes. *Heterojapyx tillyardi* from Queensland, Australia. Original drawing.

FIGS. 8–12. Examples of pterygote legs with annulated exites (EX, arrows), showing that insects are not uniramous and in the "Uniramia" of Manton (1977), but originally possessed polyramous legs along with other arthropods. Figs. 8 and 9. Paleodictyoptera, Homoiopteridae; upper middle leg in semiventral view under different illumination. Note trochanter (TR) and prefemur (PFE) fused together but still separated by a suture. The prefemoral exite (arrow) in prefemoro-femoral membrane is faintly annulated. The femur has an inflated femoral head. Fig. 10. Interpretation of the free thoracic leg of Paleodictyoptera. The trochanter (TR) and patella (PAT) are still separated by a suture; the basitarsus (BT) is slanted as in Archeognatha; the tarsus (T) is specialized and divided into four subsegments rather than two. Together with the epicoxal and subcoxal segments, both embedded in the pleural body wall, the original pterygote leg is most probably composed of 11 segments. Homoiopteridae, *Monsteropterum moravicum* Kukalová-Peck, 1972, holotype; middle leg, length about 29.5 mm. Lower Permian strata of Moravia, Czechoslovakia. Original drawing from the holotype. Figs. 11 and 12. Ephemeroptera, Protereismatidae, isolated leg of a large specimen. The large three-dimensionally preserved coxal exite (EX) is distinctly annulated as in the Crustacea. The prefemoral exite is fragmentary. Specimen No. 8585 (Museum of Comparative Zoology, Harvard University, Cambridge); Lower Permian strata of Kansas. Original drawing.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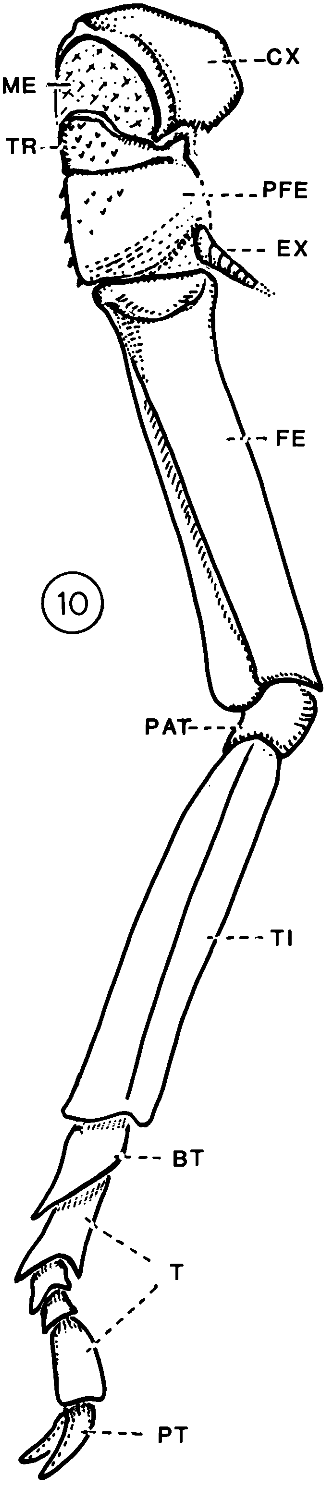
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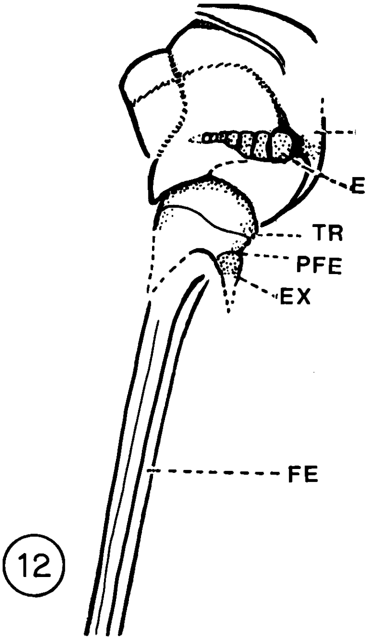
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thoracic coxae (Sharov 1966; Smith 1970; Manton 1977). Coxal styli are not developed at hatching, but occur later, after a few moults (Boudreaux 1979). This circumstance shows a coincidence with the fact that, in a primitive ontogenetic series, the thoracic wing buds are also not yet developed at hatching, but occur only in later instars (Tower 1903; Bocharova-Messner 1959, 1965, 1968; Dürken 1907). It is of interest that the coxal exite in Archeognatha is still functional and is used as a tactile device in crevices (Smith 1970).

A coxal spine occurs on the legs of Orthoptera, in Tettigoniidae (on forelegs in 10 subfamilies, on hind legs in 4 subfamilies) and in Haglidae, in *Cyphoderris*, on the forelegs (D. C. F. Rentz, personal communication). This orthopteroid coxal spine is possibly a reduced coxal exite, perhaps with some residual sensory function. There is a possibility that additional exites disguised as spines and bulges will be discovered in other modern insects.

The close structural bond between wing and spiracle (see Kukalová-Peck 1978 for references) seems to suggest that the pro-wing was originally engaged in respiration. Other possibilities are thermoregulation (Douglas 1980) or epigamic display (Alexander and Brown 1963).

With the generally accepted fact that the direct flight muscles were leg muscles originating deep in the body on the subcoxa, coxa, and sternum (Snodgrass 1935) there is little chance that the wing arose as a secondary flap, spur, or gill which were amuscular or provided only with very short muscles. Both the coxal exite (stylus), correlated with the wing in the "stylus theory" by Wigglesworth (1973), and the subcoxal exite, considered as a possible wing homologue by Rasnitsyn (1981), are also unlikely candidates. Exites in living arthropods lack musculature. Even if we accept another unlikely assumption, that the stylus drifted proximally through a whole segment or two (for what adaptive reason?) and settled dorsally, completely disattached from its segment, the exite by itself would not possess sufficient musculature.

In several crushed paleopterous nymphs from the Upper Carboniferous of Mazon Creek, Illinois, dorsal and ventral sclerites occur as a flattened ring around the wing base (my personal observations in the Field Museum, Chicago, 1980). A similar ringlike arrangement of sclerites around the wing base can be seen in recent odonates; a "smoothed out" and fused ring surrounds the wing pads of juvenile peloridiid bugs and is separated from the tergum by a suture (Evans 1939, p. 144). Similar sutures delimiting wings are found in Permian homopteroid nymphs (i.e., specimens 1700/3180 and 2494/18, Paleontological Institute, Academy of Sciences, U.S.S.R., Moscow).

Pivotal to the problem, naturally, is the origin of basalaria and subalaria. These sclerites are generally believed to be subcoxal fragments (Snodgrass 1935). However, this interpretation was certainly made with the paranotal theory in mind, and it does not agree with events observed in ontogenetic development. Thus, the basalare in modern ephemerid nymphs is born *dorsally*, as fused together with the rest of dorsal articulation (E. L. Smith, personal communication). Bocharova-Messner (1965) showed that the subalare in *Baetis* (Ephemeroptera) first appears in the membrane *above* the pleuron (subcoxa) of the 14th instar as a focus of sclerotization, i.e., does not separate from the subcoxa.

Matsuda (1970) mentioned that the subalare is formed in embryos at the "tergum." A subalar–coxal muscle was found attached to the "lateral area of the tergum" in embryos and young nymphs of a cockroach *Leucophaea surinamensis* and early nymph of *Locusta migratoria manilensis*, and later the subalare was formed by membranization around this muscle attachment. When the insect wing is absent or weakly developed, subalar–coxal muscles arise from the "lateral area of the tergum," *but not from the subcoxa* (Matsuda 1970, pp. 68, 69). Since the "lateral tergum" is in fact a fused dorsal articulation (i.e., transformed dorsal epicoxa) all the above mentioned data suggest that in the ontogenetic development of modern insects the basalare and the subalare originate with the epicoxa. Fusion of the nymphal epicoxa with the tergum is a secondary adaptation of nymphs to overcome the rigors of juvenile life (Kukalová-Peck 1978). The fact that the dorsal and ventral wing articulation are being born next to each other and distributed around the wing is probably best explained by a segment (epicoxa) that surrounded the original exite like a horseshoe (Fig. 4).

In thysanurans, wing evolution was probably arrested at the pro-wing stage, because no remnants of functional flight musculature have been detected (Kukalová-Peck 1978). However, thysanuran thoracic "paranotal lobes" have tracheation which shows a pattern similar to the venation of pterygote wings (Šulc 1911). They may represent a fusion between the epicoxal segment and an arrested pro-wing equivalent. In archeognathans, the pro-wing stood no chance of evolving, because the pleuron did not become fully incorporated to lend support to wing pivots. Therefore, the machilid "paranotal lobe" is probably represented by an epicoxa fused together with an extremely primitive pro-wing. Maybe this is the reason why the ventral part of the epicoxa remained in living machilids as a sclerite and is found under the "lobe" (Manton 1977, Fig. 9.9).

In conclusion, there is circumstantial evidence indicating that insect wings are of pleural origin; were primitively movable appendages; were primitively serial on three thoracic and nine abdominal segments; were primitively tagmatized in size, shape, and position on the segments and in function; and evolved from the uppermost arthropodan podomere, the epicoxa, and its exite. The epicoxa became incorporated into the pleural body wall in the thorax and abdomen. In the thorax, it broke into a ring of dorsal and ventral sclerites enclosing the pro-wing. The pro-wing flattened into a broad, laterally symmetrical, respiratory gill which became veined and fluted and eventually turned into wing.

Fusions between (epicoxal) dorsal sclerites and the tergum, (epicoxal) ventral sclerites and the subcoxa, and any (epicoxal) sclerites and the wing exite happened repeatedly in both juveniles and adults and are all secondary.

Abdominal winglets of fossils

Abdominal winglets of fossils are found shifted posteriorly, articulated to the (keeled) epicoxa. Since formation of the abdomen took place in hexapod ancestors before the ascent of pterygotes, the winglets very likely did not pass through a "symmetrical phase" and never participated in flight. However, they have sometimes assisted in forward movement, as they still do in Recent mayfly nymphs; modern locusts have a residual abdominal neural system engaged in (wing) movement (Robertson *et al.* 1982).

In Paleozoic mayfly nymphs, the winglets are either flat and reminiscent of miniature wings, or are more or less tubular (Kukalová-Peck 1968). If wings are indeed homologous to epicoxal exites, as discussed previously, then a tubular shape would be more primitive. Thus, the most primitive pterygote abdominal "winglet" to match this new hypothesis of wing origin would be a tubular annulated exite. In fact, exites in this evolutionary stage occurring together with a series of nine pairs of abdominal legs recently have been found fossilized (Figs. 4, 29A, 29B).

In the abdomen, the epicoxa (not the subcoxa, as erroneously interpreted by Kukalová-Peck 1978) is deformed and expressed primitively as a keeled lateral lamella. Abdominal winglets are articulated to it posteriorly on nine segments (Kukalová-Peck 1978). The 10th segment in all pterygotes so far known lacks appendages (except for the residual limb buds, which are transient in some embryos (Matsuda 1976; Boudreaux 1979)).

Abdominal winglets are still preserved in modern juvenile mayflies and are called "gills," "plate gills," or "tracheal gills." These are moved by intrinsic pleural muscles, which originate on the subcoxo-coxo-trochanteral plate (Birket-Smith 1971; Kukalová-Peck 1978, Fig. 25A). According to Matsuda (1976, 1981) these muscles are homologous to the subalar wing muscles. Wootton (1981*a*) noted that "the similarity of mayfly gills to wings is logical and may be entirely convergent"; however, no ordinary blood or accessory tracheal gills are known to be attached to muscles of an appendageal type. Because of their intrinsic musculature, articulation, segmental seriality, and position at spiracular level, serial plate gills of mayflies can be theoretically interpreted only as either exites, winglets, or legs.

Birket-Smith (1971) concluded, from study of original dissections, that mayfly tracheal gills are exites, and that two small "segments" at the base of the gill might possibly be remnants of the telopodite. The exite interpretation is supported by data introduced in this paper. The "segments" might be equivalents of basalaria and fulcalaria, possibly with an attached epicoxal fragment corresponding to the subalare. I recently found serial telopodites, situated much lower ventrally, in a giant Upper Carboniferous mayfly nymph from Bohemia. They occurred on nine abdominal segments together with the winglets, were segmented and stylus-like, and were articulated postero-ventrally at the subcoxo-coxo-trochanteral plate as are the nine abdominal telopodites of Diaphanopterodea. The last pair was transformed into claspers. This finding (now in preparation) provides the positive proof that tracheated appendages of modern Ephemeroptera cannot be legs, but are wings.

Another example of abdominal winglets is the Paleozoic neopterous nymph of plecopteroid type with abdominal wings and possibly also legs (specimen 8593*ab*, Museum of Comparative Zoology, Cambridge) (Kukalová-Peck 1978, Figs. 35, 47). I also examined all available specimens of *Eucaenus ovalis* from the Upper Carboniferous of Mazon Creek, Illinois, classified by Carpenter and Richardson (1976) as Protorthoptera. The "abdominal lobes" described on their Figs. 2 and 8 are in fact annulated exites articulated in the same locus as abdominal tracheal winglets of mayfly nymphs (Figs. 29A, 29B); abdominal legs of *Eucaenus* appear to be reduced to a swelling in the posteroventral corner of the subcoxo-coxo-trochanteral plate (abdominal pleuron). This condition is close to modern embryos of Megaloptera (Fig. 2A). According to Miyakawa (1979), the embryo of *Protohermes grandis* shows two series of swellings on the 5th day: dorsal swellings which later give rise to eight pairs of tracheal gills, and ventral swellings serially homologous with pleuropodia, which later stop developing. Pleuropodia are glandular modifications of legs (Norling 1982, and references therein) and become conspicuous on the first abdominal segment on the 8th day. Tracheal filaments of megalopteran larvi are very probably homologous with the annulated exites of *Eucaenus ovalis*; they are similarly shaped but the annulation became obliterated.

Norling (1982) published a detailed, very informative study of abdominal tracheal filaments in the nymphs of Euphaeidae and Polythoridae (Odonata: Zygoptera). Three possible interpretations were offered and, at the same time, disputed: (*i*) origin as secondary, independent structures; (*ii*) origin from limbs; and (*iii*) origin from wing homologues. Data assembled by Norling are explained here as follows.

The secondary origin is highly unlikely, because the filaments are segmental, are borne in the same locus (at the level and behind the spiracle), and have similar shape, structure, and function not only in Zygoptera, but also in Ephemeroptera, Plecoptera, Megaloptera, and possibly also in sisyrid Neuroptera, and in gyrinid Coleoptera. All these groups are considered to be generally primitive[5] and, at the same time, have in all probability primitively aquatic nymphs. The plesiomorphic character of tracheated appendages in general, and especially tracheated *segmental* appendages, was assembled and phylogenetically evaluated by Štys and Soldán (1980). Filaments are clearly of pleural origin and serial, and follow a pattern similar to abdominal limbs. They also have leg-type muscles attached to their bases at least in Zygoptera and Ephemeroptera. As opposed to this, secondary, simple gills and accessory gills always lack musculature. There is a deep structural difference between segmental and other gills even if they both perform the same function.

Origin from limbs is quite improbable because filaments occur dorsally from pleuropodia, and in a Carboniferous protodonate nymph (specimen PE 3072, Field Museum of Natural History, Chicago, Figs. 30A, 30B) filaments occur also on the *same* first abdominal segment as pleuropodia. These are known to be serial with limbs. In the three embryonic series of appendages known in endopterygotes (Miyakawa 1979) (filaments, limbs, endites), the pleuropodia are in the middle. The fact that in groups other than Ephemeroptera the filaments seem serial with the thoracic legs in effect contradicts this seriality, as follows. As shown in Figs. 4 and 30, the pterygote abdominal pleuron consists of three incorporated segments, while the thoracic pleuron has only one. Hence, the abdominal limb starts with a prefemur and is placed relatively more ventrally. In all fossil pterygotes which have preserved abdominal limbs, these start at the posteroventral corner of the pleuron (Fig. 1), at the same level and place as male gonopods (claspers). Therefore, thoracic and abdominal legs are primitively arranged in different levels and are *not* aligned. This condition is also well expressed in primitive modern embryos (Figs. 2A, 2B). In 1978 I erroneously considered the spiracle as a landmark for wings (above) and legs (below) the spiracular level. In fact, wings are borne at the level of and behind the spiracle, but during development they can migrate upward or down somewhat. Under the circumstances, the leg character of musculature and occurrence in the limb area, mentioned by Norling, is best explained by interpreting the filaments as leg exites.

An origin from wing homologues stands out as being very likely, if the filaments are seen as evaginated beyond spiracles, articulated above the leg series and moved by leg muscles, which is what they are, rather than respiratory evaginations of a fine pleural membrane, which is how they function. The difference between Odonata and Ephemeroptera in muscles attached to the filament base is best explained by the fact that both types are residual and were derived from a general plesiomorphic condition rich in musculature. The "segmentation" of filaments is well expressed especially in the polythorid damselflies and is perhaps accompanied by some weak musculature entering the appendage (Norling 1982). This cannot be true segmentation but is transformed annulation, because primitive pterygote exites (Figs. 8–12 and 29A, 29B) are annulated. Large setae, described by Norling, that occur on segments VIII and IX on the same locus as gill buds are probably serially homologous with the peculiar prominent setae on thoracic wing buds, described previously by Bocharova-Messner (1959).

Occupation of dry land

In every hypothesis of wing origin the transition between the aquatic and the terrestrial habitats is of primary importance. According to Hinton (1953), Boudreaux (1979), and others, the ancestors of Tracheata did not evolve tracheal respiration until some time after complete or partial transition to terrestrial habitat. During the aquatic existence, they presumably respirated with the help of blood gills. This presumption may apparently be a serious misconception. A thoroughly assembled and richly documented paper supporting the aquatic origin of tracheated structures through their modern occurrence and function was recently published by Štys and Soldán (1980). The authors documented that most primitive living insect orders have aquatic juveniles with closed tracheal systems and plesiomorphic, tracheated, and segmental appendages that could have persisted only in an aquatic or extremely wet environment. This coincidence is not accidental. Štys and Soldán (1980) outlined a hypothetical evolutionary mechanism which lead to the origin of aquatic tracheal respiration; they concluded (p. 432) that apneustic spiracles were probably at first only sites of embryonic or early postembryonic invagination of tracheal tissue and where the tracheal intima got pulled out. Prespiracles and the tracheal system were preadaptations for a shift of propterygotes (more likely, of protracheates) to an amphibious life.

As far as the conversion of a movable appendage into a gill is concerned, the aquatic habitat was probably

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[5] Gyrinidae are newly considered as a possibly primitive family by J. F. Lawrence (personal communication in 1982).

necessary for the preadaptation of the flight-promoting movements. Aquatic respiration is a common function of the upper leg exites of living Crustacea. Myriapoda, lower Insecta, and Pterygota alike have residual exites on the upper leg segments. Tracheal gills of modern mayflies, the muscles of which are serially homologous to those of the wings, are still engaged in underwater breathing and in forward locomotion, all with closed spiracles. There are tracheal filaments, homologous with abdominal wings, in megalopteran, neuropterid, and possibly also coleopterid larvae, plecopteran nymphs, and in some odonatan nymphs.

It seems that the clues to the aquatic origin of the tracheal system may still be present in modern insects. The surviving primitively aquatic juveniles still take dissolved oxygen directly from the water through tracheated surfaces, and this underwater tracheal breathing takes place *before* the spiracles are opened. As proposed by Štys and Soldán (1980), the opening of spiracles only provides the necessary "switch" for the underwater breathing system to be used also on dry land.

Note that Crustacea, the sister group of the Tracheata, already occur in the Cambrian. For that reason, both groups must have been established in the early Cambrian at the latest, but more probably in the Precambrian (Hennig 1981).Tracheae of myriapods and insects are homologous and are the apomorphic character of the group. This homology was recently confirmed again by E. L. Smith (personal communication). In the Precambrian and Cambrian, there were probably no terrestrial plants to sustain life on dry land. Therefore, prototracheates are believed to be aquatic animals. At the same time, we have evidence that the main subdivisions in tracheates happened early perhaps in Ordovician, because specialized collembolans, remnants of dicondylates and of archeognaths, occur already in the Lower Devonian (Hennig 1981, and unpublished fossil record). Therefore, it is very probable that Cambrian protracheates already had (aquatic) trachea.

Hinton (1953) argued that terrestrial adaptations of generalized (modern) tracheates (myriapods and lower insects) proves that the tracheae themselves originated on dry land. This argument would be meaningful only if Hinton could have shown that *ancestral* lower tracheates, possibly in the Ordovician, were fully terrestrial. Unfortunately, fossil evidence is lacking. As far as the available data are concerned, the gigantic Carboniferous myriapods, the arthropleurids, are usually considered to be amphibiotic. The fossil record on the oldest machilids is wanting but modern bristletails often live in a wet environment; especially interesting is their occurrence on the seashore just above high tide (Australian *Allomachilis*; European *Petrobius maritimus* and *P. longicaudatus* inhabit the marine splash zone in great masses feeding on blue-green algae). It is therefore possible that these "semiaquatic" machilids still live in or near to the plesiotypic environment.

The most important evidence contradicting Hinton's view is, however, the following. In 1975 and 1977 I found large quantities of primitive silverfish from the order Monura (close to 400 specimens, mostly juveniles representing about 30% of all insect remains) in aquatic deposits of a late Carboniferous river delta in Carrizo Arroyo, New Mexico. Monura cannot fly or be windblown and are too fragile to withstand transport from land by water runoff and streams. Most specimens were found almost complete, frequently as exhuviae. The most likely explanation of this kind of preservation and occurrence in paleontology is that juveniles lived and died where they were found, i.e., in the aquatic environment. Thysanuroidea are the sister group of Pterygota, in which most of the generalized orders (the Paleoptera, and the orders at the base of the Neoptera and Endopterygota) *also* have aquatic juveniles. This coincidence makes a strong case for the plesiomorphy of a "closed" tracheal system.

In seemingly the most probable scenario, ancestral tracheates possibly had aquatic juveniles and amphibiotic adults already when the split occurred into myriapods and insects (in the Ordovician?). Myriapods and insect-endognaths independently and gradually became terrestrial in adults and juveniles, but some insect-ectognaths retained aquatic juveniles. Thysanuroids maintained aquatic juveniles in the Paleozoic, but changed to a fully terrestrial life in the Mesozoic. Most generalized pterygote orders retained aquatic juveniles with a "closed" tracheal system (i.e., functioning underwater), and tracheated, leg-derived, segmental, underwater breathing appendages until present times.

I suggest that spiracles probably developed from the ecdysial sites only once, in the protracheates, before the split into Myriapoda and Insecta. At first, functional spiracles were limited only to adults, subadults, and older nymphs. In modern generalized insects some of these instars are fused into the metamorphic instar.

Tagmatization into the head, thorax, and abdomen is the basic apomorphic character which differentiated Insecta from Myriapoda. Tagmatization must have occurred after the origin of tracheae and possibly after conversion of ecdysial sites into spiracles in the adults, at the stage when epicoxal exites were still primitive, not reduced and not fused with the terga. In the protracheates, the epicoxal exites flattened into respiratory flaps. In the insectan lineage these flaps were originally probably used as ventilating devices. However, in the myriapods, and later also in insect-endognaths and lower ectognaths these flaps stopped functioning and became fused with their surrounding epicoxa in a lobe called a paranotum, which probably protected legs. The paranotum originally was separated from the tergum by a deep suture (Figs. 5, 6). The suture later disappeared, and the paranotum became unrecognizeable from tergal lateral lobes of arthropods, called paraterga.

In the ancestral pterygote lineage with aquatic juveniles, the ventilating respiratory flaps eventually became more mobile and helped in underwater swimming. This forward movement played a critical role in preadapting the pro-wing blade for flight, in preparing flight musculature, and in fissuring the epicoxa into articular sclerites surrounding the pro-wing base. In terrestrial pterygote adults the pro-wings initially served perhaps as pushing devices, which also helped to extend free fall from heights by a flapping motion. Later on, the rowing pro-wings in aquatic juveniles became successively streamlined, immobilized, and tucked away on the back, while wings in the adults grew in size and became flight adapted. The splitting of pterygotes into Paleoptera and Neoptera, as well as the diversification of major lineages happened simultaneously with flight adaptation, while still at the stage of an almost symmetrical pro-wing.

The pro-wing and wing venation

Primary wing veins are not random thickenings of the wing cuticle which evolved in the process of flight adaptation, but are a residual, transformed sections of the flattened pro-wing lobe after it became fissured for more flexibility. The fissuring delimited the blood channels inside the sections; the channels continued under the basal articular sclerites and opened into the body cavity. Tracheae penetrated the wing through the blood channels.

Almost certainly, the pro-wing lobe was originally densely filled with dichotomously branched primary veins (Fig. 13) for three reasons: (*i*) primitive Paleozoic wings of all lineages show rich or very rich and dichotomous venation (Kukalová-Peck 1978 and see references therein, Kukalová-Peck and Richardson 1983; Figs. 6, 9, 12A, 14–23); (*ii*) theoretically, dichotomous branching is the simplest way for a channel system to fill out a lobe; and (*iii*) articulated, movement-promoting, flattened leg appendages of crustaceans (uropods of the Decapoda), which seem to be morphologically close to plesiomorphic wing characters compiled in Paleozoic insects,[6] are adapted for swimming: they are almost bilaterally symmetrical lobes in shape, densely filled with dichotomously splitting veins, and they carry several irregularly distributed folds, and the equivalent of an "anal" area. Each lobe has a serrated outer margin where veinal branches dissect it at an angle. All these features, including the serrated margin, occur primitively in haustellate Paleoptera, Paleozoic Ephemeroptera, and Odonatoidea, as well as in most primitive known Neoptera of the plecopteroid stem group.

As discussed earlier, the pro-wing lobe probably developed from an annulated tubular appendage, an epicoxal exite, that became flattened and changed into a respiratory exite when insects were still aquatic (Štys and Soldán, 1980). The pro-wing lobe was probably at first soft and filled with richly branched tracheae, which were pulled out during moulting through the protospiracles located anteriorly and under the pro-wing lobe. It is worth mentioning that apparent absorbing of aerial oxygen through the tracheated lamellar gills was recently observed by G. B. Montieth (personal communication, 1982): Recent odonate nymphs of *Podopteryx selysi* (Megapodagrionidae) of North Queensland, Australia, live in tree holes with a wet anaerobic organic sludge. At night, they spread the caudal gill lamellae at the water surface with the upper side of the gills exposed, presumably to obtain oxygen directly from the air.

The adaptive reason why the lobe stiffened and broke up into sections (the protovenation) was probably to attain flexibility during motion, as in crustacean uropods. Perhaps respiratory lobes became engaged in ventilation, thermoregulation, and (or) epigamic display and this triggered their later transformation into wings.

The functional and morphological analogy with modern uropods seems to indicate that venation is not a "speciality" of the pterygotes, but the way in which arthropodan lobes became adapted for promoting movement. It also indicates why the insect veins consist originally of two sectors: because splitting of the lobe into sections started immediately at the base and was dichotomous. However, compared with crustaceans, the flexibility and firmness of each paired vein in ancestral pterygotes was further enhanced by alternate fluting of the sectors. Fluting of veins in the uropods is inconspicuous and is restricted to few areas.

The flexible parts of the lobe were probably at first only grooves between the protovenation. Eventually, these became widened and thinned. The thinning left behind a meshwork (an archedictyon). It should be noted that an archedictyon occurs primitively in the wings of all Paleoptera (including primitive odonatoids) and Neoptera, but is not limited only to pterygote wings. The cuticular surface of the body and limbs of some crustaceans (i.e., some crabs) carries a meshwork pattern that is also found on the body of some pterygotes (i.e., some true bugs). Apparently, a meshwork is a

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[6] Previously, uropods of Devonian crustaceans were thought to be, by some entomologists, the wings of early pterygotes, so close is their protovenation to that of the wings of cockroaches. The protovenation in modern crustacean uropods is best seen in decapod exuviae.

general arthropodan quality of the cuticle, which may express itself when the cuticle is thinner.

Wing articulation and the new articular band hypothesis

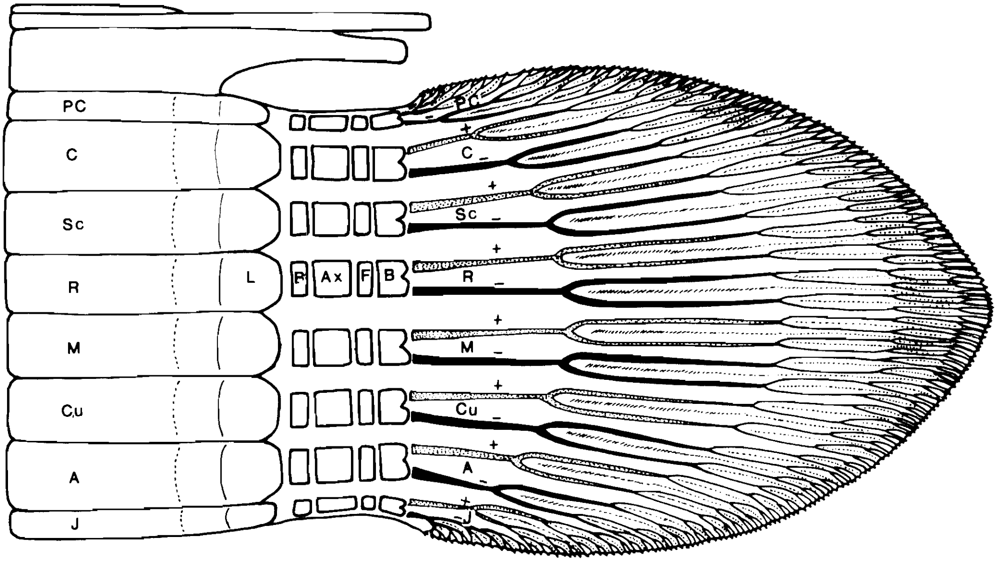
Modern wing articulations serve roughly three kinds of flight: odonatan (with direct musculature), ephemerid (with a peculiar mixture of direct and indirect musculature), and neopteran (with indirect or sometimes mostly direct musculature combined with wing folding) (Boudreaux 1979). All the varied types of flight musculature diverged from the common ancestral type, which was a mixture of direct and indirect muscles (Boudreaux 1979). At the same time, wing shape and venational pattern in all insects responded to the same aerodynamic laws. Owing to conflicting evolutionary trends, wing articulation has been subject to a very complicated adaptation which was deeply influenced by convergence. In the process, the ground plan articulation of pterygotes became obscured in modern insects.

Since the primary venational pattern is shared by all pterygotes (an almost general belief), there must have once existed a common pterygote articulation ground plan. The monophyletic origin of wings also means a monophyletic articulation, because wings and their moving structures could not have originated independently. In the fossils the immediate relation between the wing veins and articulation is convincingly expressed by the fact that in all primitive wings the articular sclerites are aligned with the veinal pairs (Kukalová-Peck and Richardson 1983, their Figs. 3–5, 7, 11, 12A; Figs. 3, 13, 15, 16, 22, 24 in this paper).

In addition to six veinal pairs documented previously (Kukalová-Peck 1978), the better preserved specimens of large homoiopterids also show precostal and jugal rows of sclerites. These are aligned with the serrated margin anterior to costa which represents the reduced precostal pair, and with branched jugal veins in a separate jugal area (Kukalová-Peck and Richardson 1983, Figs. 5, 11). There is, therefore, a good reason to anticipate that before the costal margin became adapted for forward flight, the precosta was symmetrical to other veins; likewise, jugal veins, which had not been previously recognized in Paleoptera, should be added as the eighth veinal pair occurring primitively in all Pterygota. The tegula is a trichobothrium, not a sclerite (E. L. Smith, personal communication), and has nothing to do with articulation (contrary to Kukalová-Peck 1978 and others).

Herein, veinal symbols are altered to agree with the fact that each vein is originally composed of two sectors, an anterior (A) and a posterior (P): the posterior radial sector is called RP (not Rs), the anterior anal sector AA (not 1A), the posterior anal sectors AP (not 2A or 3A),

FIGS. 13–15. Models of composites of preflight (plesiomorphic) and postflight (mildly apomorphic) characters intended to show, by double comparison, specialization of veinal characters in living insects. Fig. 13. Hypothetical, more or less symmetrical nonflying pro-wing showing plesiomorphic branching of veins; veinal pairs, proarticulation, and tergal lobes were aligned with each other; the outer margin was probably serrate, veinal sectors were dichotomously branched three or four times and mildly fluted, and interveinal spaces were double fluted (dotted lines). Each pair of veinal sectors shared one blood duct under each row of articular sclerites composed of proxalaria (P), axalaria (AX), fulcalaria (F), and basivenalia (B). Tergal lobes (L) articulated with eight proxalaria; 16 veinal sectors articulated with eight basivenalia. Remnants of symmetrical features, postulated here as preflight in origin, occur in abundance in primitive Paleozoic pterygotes and are scattered and less conspicuous in the living forms. Fig. 14. Three major evolutionary trends occur in pterygote veinal pairs. Primitively, two mildly fluted, convex anterior and concave posterior sectors are hinged to the basivenale (B) branching dichotomously three or four times. Later, sectoral stems become adjacent (as RA and RP stems in Odonata) or superimposed (as RA stem in Ephemeroptera), or superimposed and the convex sectoral stem reduced (as M− and CU− veinal stems in homoiopterid Paleodictyoptera). Terms: a veinal pair is composed of two sectors, starting from the same basivenale; a veinal stem is composed of two sectoral stems; first sectoral branches (′, ″); second sectoral branches (1, 2, 3, 4). Original drawing. Fig. 15. Model of composite flying wing with early changes towards asymmetry that accompanied flapping flight. These changes are much more evident in fossil forms than in modern pterygotes. PC, C, and ScA lost most branches and became fused in the costal margin. ScP and R became axial supporting veins; R, M, and Cu fused basally into veinal stems (stripes); CuP lost most branches and narrowed to become a flexion line in flight; AA and AP almost lost sectoral stems, bundled and fanned out to make the anal area pliable; dichotomous branching became asymmetrical and reduced; numerous braces (BR) appeared from diverse interveinal fusions; cross veins (*cr*) and bars formed from the archedictyon complemented veinal braces. Asymmetrical folds evolved, cut through the veins, and changed their fluting. The costal margin, hinged to basalaria via precostal sclerites, was pulled down by basalar muscles for pronation. The originally mild, regular fluting of sectors changed to neutral or stronger fluting, and sometimes even became secondarily reversed. Original fluting of the membrane mostly disappeared, but sometimes persisted and became supported by intercalar veins. Original archedictyon became mostly reduced, but the secondary archedictyon, branches, cross veins, and secondary fluting of the membrane sometimes appeared to replace reduced primary venation, especially if wings increased in size. Tergum developed large radio-medial lobes (shoulders, L), and notches at the cubital level. Some sclerites of the articular band fused into axillary plates (in Paleoptera) and into axillary sclerites (in Neoptera), and some in Neoptera became associated with the tergum as "processes." Original drawing.



13

PC
C
Sc
R
M
Cu
A
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PC
C
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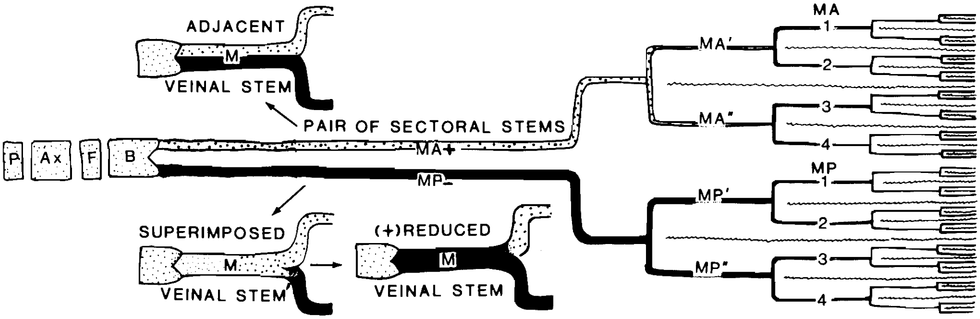

14

ADJACENT
M
VEINAL STEM
PAIR OF SECTORAL STEMS
P
Ax
F
B
MA+
MP–
SUPERIMPOSED
M
VEINAL STEM
(+)REDUCED
M
VEINAL STEM
MA
MA'
MA"
1
2
3
4
MP
MP'
MP"
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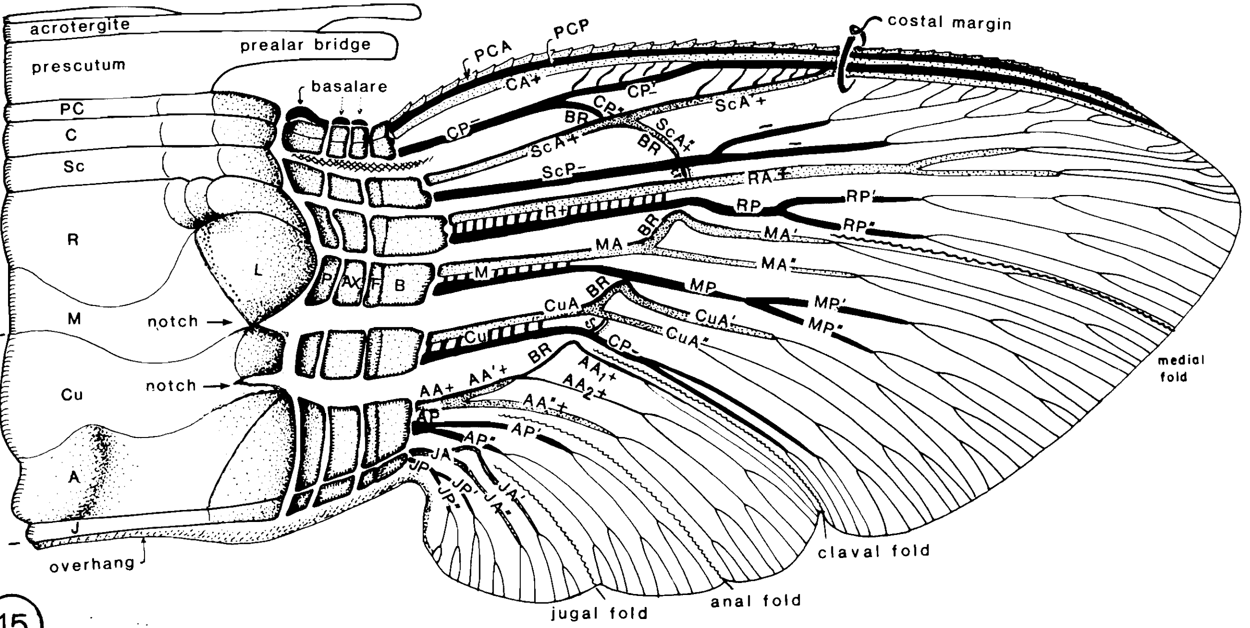
4



15

acrotergite
prealar bridge
prescutum
PC
C
Sc
R
M
Cu
A
J
scutum
scutellum
notch
notch
overhang
L
basalare
P
AX
F
B
PCA
PCP
CA+
CP–
CP'–
CP"+
BR
ScA+
ScA'+
ScA"+
BR
ScP–
RA+
R+
RP
RP'
RP"
MA
BR
MA'
MA"
M
MP
MP'
MP"
CuA
BR
CuA'
CuA"
Cu
CP–
BR
AA+
AA'+
AA₁+
AA₂+
AA"+
AP
AP'
AP"
JA
JA'
JA"
JP
JP'
JP"
costal margin
medial fold
claval fold
anal fold
jugal fold

and the posterior subcostal sector ScP (not Sc), etc. (see Figs. 13, 14, 15).

Paleozoic representatives of all paleopterous orders show an articulation in which many sclerites are individually delimited by sutures and that presumably is closer to the ancestral condition. Articulation of the most primitive, haustellate, phytophagous Paleodictyopteroidea, namely of Paleodictyoptera and Diaphanopterodea, is so simply organized that it seems almost equal to the ancestral state. Paleozoic Ephemeroptera and Protodonata show an intermediate type between the paleodictyopteroid and modern paleopterous articulation; this reinforces the conclusion that the paleodictyopteroid type is extremely primitive.

The presumed ancestral articulation is a simple, broad band extending between the wing and the tergum and apparently continuing ventrally under the wing on both sides as basalaria and subalaria. In its dorsal part, the band is fissured into eight rows of 4 sclerites, which are aligned with eight veinal pairs (Figs. 13, 15), altogether 32 sclerites. All band sclerites are densely adjacent. Muscle scars, found occasionally imprinted in scalped sclerites, indicate that originally probably all sclerites except basivenalia (see below) received muscles. The whole articular band gives an impression that it was derived from a complete segment (leg segment) which became first incorporated into the body wall and then fissured around and along the inserted intrinsic and extrinsic leg muscles.

The model of the primitive pterygote articular region introduced here (Figs. 13, 15) had to be done in two steps, to reflect the variable evolutionary combinations of features of the pro-wing and the flying wing: as a schematic model of a hypothetical, near-symmetrical pro-wing (Fig. 13), and as a schematic model based upon paleodictyopteroid articulation and compiled major trends of venational adaptation (Fig. 15). It should be noted that a modern insect wing represents an intricate, varied mixture of plesiomorphic (symmetrical) elements, and apomorphic (asymmetrical) elements. These combine differently in different lineages and bear testimony that the split and subsequent radiation of Pterygota happened at the latest in the late pro-wing state. Otherwise it would not be possible to explain why each lineage has its own and somewhat different solution to the same set of aerodynamic problems, and why preflight, symmetrical venational characters survived, scattered, in unrelated modern groups, as will be discussed later.

Sclerite nomenclature

The nomenclature of the articular band is based mainly on the articulation of extremely large Paleodictyoptera: Homoiopteridae, from the Middle Upper Carboniferous of Illinois, which are described by Kukalová-Peck and Richardson (1983); (Figs. 16A, 16D).

The following new names are proposed for the 32 ancestral sclerites (see models, Figs. 13, 15) in the dorsal band of pterygote wing articulation.

Columns of sclerites

Basivenalia: The sclerites of the most distal column of sclerites are called basivenalia (B) (singular, basivenale). Veinal bases, represented either by two stems of sectors (sectoral stems) or by one fused veinal stem, are hinged or fused to the basivenalia (Fig. 14).

Fulcalaria: The next proximal column of sclerites are fulcalaria (F), (singular, fulcalare[7]) which were recognized and named by E. L. Smith (personal communication) (Fig. 14). Fulcalaria all had a primitive musculature and provided the pivots (fulcra) for wings of Pterygota. Serial muscle scars on fulcalaria are known in Paleozoic Ephemeroptera (Fig. 3, ⊗). Fulcalaria pivot on VWP and on ventral sclerites, basalaria, and subalaria (E. L. Smith, personal communication).

Axalaria: The next proximal column of large sclerites is called axalaria (AX) (singular, axalare).

Proxalaria: The proximal column of sclerites, the proxalaria (P) (singular, proxalare), are the most varied in shape, length, and width.

Rows of sclerites

The simplest and most comprehensive way to name the sclerites in transverse rows is by using the classical names of the veins. There are thus four precostal, four costal, four subcostal, four radial, four medial, four cubital, four anal, and four jugal articular sclerites. Each individual sclerite can be indicated by using the name of the row as an adjective and the column, as a noun, i.e., medial axalare, radial fulcalare, precosto-costal basivenale, etc.

Alignment between sclerites and veins was functionally necessary and must be as old as the veinal system. Wing veins are primitively blood lacunae and dorsal sclerites kept open the blood passages between them and the body (Arnold 1964).

Homoiopterid articular band and functional units

The wing base of the homoiopterids (Figs. 16A, 16D) is divided into two functional units, one composed of hinged sclerites and the other of hinged and fused sclerites. In the hinged unit, the precosto-costal vein is movably hinged to the precosto-costal row of four sclerites, the most proximal of which (precosto-costal

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[7] According to linguists, there is considerable freedom in forming new scientific terms. However, speech esthetics is highly commendable. Fulcralare (from "fulcrum") may be a more logical derivation but the repeated *r* and *l* combination is quite a tongue-twister and resists repetition.

proxalare[8]) articulates with the basalare (BA), a ventral articular sclerite. Muscular tension on the basalare is transferred to the wing's anterior margin and pulls it down at an angle (pronation) which is essential for forward flight.

The subcostal through jugal basivenalia are mutually fused (except in the oldest homiopterid *Ostrava nigra*) with the next proximal sclerites (fulcalaria) into a single, probably nearly inflexible axillary plate composed of 12 sclerites (Kukalová-Peck and Richardson 1983, Fig. 5). A similar axillary plate is also present in ephemeropterans (Fig. 3). The axillary plate is further fused with the axial wing vein R+ (Figs. 16A, 16D). Consequently, the plate and the R vein can move only together. ScA+ and ScP− may have been sometimes also fused with the axillary plate. Because of this, homoiopterid wings were adapted to be held in an outstretched position without the action of muscular tension (as in modern Paleoptera) so that gliding flight was effortless and locking of the wings unnecessary. This kind of flight was suited to the aerial life of paleodictyopterids and their assumed search for widely scattered food (Kukalová-Peck 1983). This adaptation is here considered to be secondary.

Sclerites in the dorsal articular band are closely packed together and are delimited from each other mostly by thin sutural lines. There is a gap between the precosto-costal row and the subcostal row (Kukalová-Peck and Richardson 1983, Fig. 11; Fig. 16A, 16D), which corresponds to the flexion line that separates the pronating anterior unit from the rest of the articulation. A deep and broad groove occurred between the subcostal and radial rows. This groove most likely allowed differential movements during flight, but its exact role is unkown. A fused axillary plate is not distinguishable in fossils with undamaged articular regions, so closely are the sclerites packed together, but some detached homoiopterid wings (i.e., Kukalová-Peck and Richardson, Figs. 18, 20) have been found with the axillary plate separated from the other sclerites and attached to the wing base. This kind of preservation is also present in representatives of other paleodictyopterid families.

The articular region is convexly bulging above the almost flat tergum. The column of proxalaria is steeply bent mesally and is separated from the column of axalaria by sutures. Posteriorly, proxalaria are narrow and there is a deep muscle scar on the cubital proxalare (Kukalová-Peck and Richardson 1983, Figs. 1, 2). Proxalaria in the paleodictyopterans look rather like a bent edge of the axalaria because of dense arrangement of all sclerites. However, in ephemeropterans as well as odonatans, in which the sclerites are divergent and separated by membranous gaps, the hinged column of proxalaria is quite apparent (Fig. 16).

The axalaria form the most convex column in the articular band while the fulcalaria are narrow and recede into a neutral position. There are several muscle scars in the axalaria of Paleozoic ephemeropterans, but none are visible in the paleodictyopterans, perhaps because of their heavier sclerotization. Fulcalaria, because of their pivoting function (they pivot on basalaria, VWP, and subalaria; E. L. Smith, personal communication), must have been originally musculated, but no distinct scars have been observed. A regular series of fulcalar scars exists in Paleozoic Ephemeroptera (⊗ in Fig. 3), and residual fulcalar musculature has been found in Recent Ephemeroptera (E. L. Smith, personal communication). Fulcalaria of modern Odonata are musculated (Figs. 16B, 16E, circles).

Basivenalia in homoiopterids are large, neutral in position, and quite variable in shape. No muscles could have been attached to them in flying wings, because the column is outside the wall of pivots and muscles cannot stretch and pull effectively over an obstacle. It may be that the basivenalia, or these and the fulcalaria, separated from the very base of the movable appendage itself. Proxalaria and axalaria dorsally, and basalaria and subalaria ventrally, are probably derived from the epicoxa as will be discussed later in this account.

The homoiopterid wing was articulated immediately posterior to the prescutum and along the whole remaining margin of the tergum. The scutellar overhang (postscutellum) became fused with the overhang of the articular band and with the posterior wing margin into a blood duct, called the axillary cord. Therefore, the primitive wing is narrower than the full length of the tergum but about as wide as the subcoxa (=pleuron; =episternum and epimeron). The subcoxa represents a whole leg segment which occurs in all other arthropods and in pterygotes is incorporated into the body wall (E. L. Smith, personal communication). The claim that the width of the primitive wing matches that of the tergum and thus provides support for the paranotal theory is therefore unfounded (Kukalová-Peck 1978).

This homoiopterid articulation is known in five specimens, all of which are shown in Kukalová-Peck and Richardson 1983. The proportions, sizes, and shapes of sclerites within members of one family may seem to be more widely variable than is the case in Recent Paleoptera. However, Paleodictyopteroidea were by far more diverse than modern Paleoptera, and their classification is based mainly on wing venation, so that the taxonomic criteria do not match those used in modern entomology.

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[8] In Paleozoic and modern Ephemeroptera, the basalare is articulated to the *precostal* proxalare; in all odonatoids, basalaria are fused to *precostal* axalare and fulcalare (Figs. 16B, 16E). Primitively, the precostal and costal rows of sclerites were probably separated (Fig. 16C). All these data support the existence of a precostal veinal pair in the pro-wing.

Gliding and wing-folding adaptations in Pterygota

Recent paleopterans (Ephemeroptera and Odonata) share the ability to glide effortlessly on wings spread out with the help of a special composite sclerite fused to the wing venation. Snodgrass (1927, 1929, 1935) named this sclerite the "axillary plate." In ephemeropterans, the axillary plate is usually called the "medial" plate. It is a composite sclerite (Kukalová-Peck 1974) formed originally by fusions of subcostal through medial basivenalia and fulcalaria, stiffly hinged with the cubital, and with anal–jugal basivenalia and fulcalaria (Figs. 3, 16C, 16F). In odonates, there are actually two composite axillary plates, the anterior and posterior. The anterior axillary plate is called by typology incorrectly the "proximal humeral plate" but is very different from the humeral plate of Neoptera. The anterior axillary plate is a composite of several sclerites. Preliminary study showed that these sclerites probably belong to precostocostal axalaria and fulcalaria, plus at least two basalaria, which fuse with the plate ventrally and anteriorly as a narrow rim. The posterior axillary plate of odonates was named the "radio-anal" plate by Tannert (1958), who saw it as a composite sclerite formed by fusions between veinal bases. In fact, this plate involves 18 sclerites: subcostal through jugal axalaria, fulcalaria, and basivenalia, as will be documented in detail in a later paper. The column of sclerites proximal to both axillary plates in Odonata belongs to proxalaria (Fig. 16B, 16E).

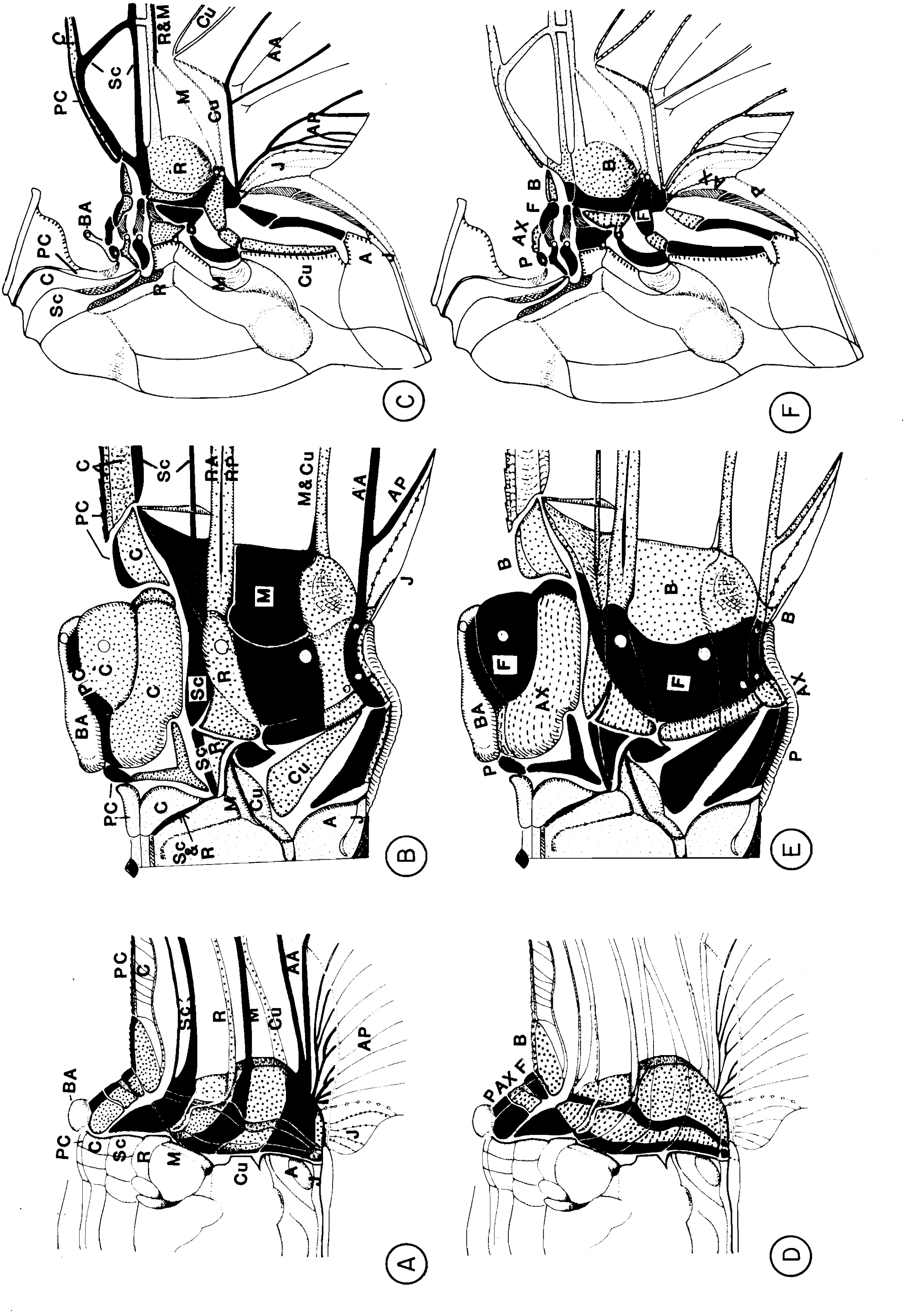
Some of the above-mentioned terms express incorrect homology: the "medial" plate in mayflies is not the medial basivenale but a composite, and does not support the media, but the stem of ScP and R; the "radio-anal" plate includes also subcostal and jugal sclerites. Therefore, the most suitable term is Snodgrass' axillary plate, defined as a "composite sclerite in the dorsal articulation of gliding Paleoptera."

In Paleozoic strata, the gliding paleopterans are always found with outspread wings: Paleodictyoptera, Megasecoptera, Permothemistida (=Archodonata), Ephemeroptera, and Protodonata. Members of the closely related (to Paleodictyoptera) but more primitive order Diaphanopterodea (the adults had nine pairs of abdominal leg rudiments like Archeognatha) were able to fold their wings backwards (Fig. 1). Outspread wings are therefore not a character shared by all Paleoptera as defined by Martynov in 1924. The mechanism behind the gliding ability in Recent paleopterans depends on an equilibrium between wing and body, attained when the axial wing veins (R, or ScP and R) become fused with the cluster of articular sclerites, the axillary plate. The rest of the veins usually stay hinged, namely the precosto-costa to the precosto-costal basivenale, and the media, cubitus, anal, and jugal to the posterior part of the axillary plate. The fusion between axial veins and axillary plate prevents wings from being folded backwards, even if the plesiomorphic wing-folding muscle, which in Neoptera is inserted into 3Ax, is present. Flight of Paleozoic insects was examined by Wootton (1976).

The "wing folding" muscle, or more accurately its homologue, was found in all Pterygota (Snodgrass 1935, p. 188; and Brodskii 1970), and is inserted in the cubital fulcalare. In modern Paleoptera, the cubital fulcalare is part of the axillary plate or eventually, stiffly hinged to it. Very likely, the same wing folding muscle, inserted probably into the same sclerite and maybe branched to some adjacent sclerites, was also responsible for folding the wings in Diaphanopterodea.

Diaphanopterodea are now becoming well docu-

FIG. 16. Paleodictyoptera, Homoiopteridae, used here as clues to interpret dorsal articulation of Odonata and Ephemeroptera. Note that articular sclerites are expressed as a band composed of four columns (P, AX, F, B), and eight rows aligned with veins. (A and D) Paleodictyoptera, Homoiopteridae, *Mazonopterum wolfforum* Kukalová-Peck & Richardson 1983, Upper Carboniferous strata of Illinois. (B and E) Odonata, Petaluridae, *Uropetala carovei* (White, 1843), Recent, New Zealand. (C and F) Ephemeroptera, Siphlonuridae, *Siphlonurus* sp., Recent, North America (this specimen was stained and observed as it dried out, not as a slide). Columns and rows of sclerites are alternately shaded for better recognition. Membranized sclerites of mayflies are obliquely lined. (A, B, C) Rows of sclerites in Paleodictyoptera are clearly aligned with eight tergal lobes and eight veinal pairs. In Odonata, the alignment is mostly preserved, but Sc and R tergal lobes are both invaginated, and Sc and R proxalaria (P) are fused; basalaria (BA) are articulated with PC proxalare, and are fused with PC axalare and PC fulcalare, anteriorly as well as ventrally, thus forming a ring around the wing base. In Ephemeroptera alignment is distorted but preserved; rows and columns of sclerites are interrupted by membranization of C, Sc, and R axalaria, and the whole jugal row is membranized. Note that PC and C rows proximally separate from each other and diverge. The ventral basalare is single and is articulated only to the end of the precostal row of sclerites. (D, E, F) Dorsal articular sclerites, proxalaria (P), axalaria (AX), fucalaria (F), and basivenalia (B) in Paleodictyoptera are clearly aligned into four columns reminiscent by the general outline of the neopteran articular region. The axillary plate is composed of Sc through J fulcalaria and basivenalia (maximum 12 sclerites or less). In Odonata, PC, C, M, and Cu proxalaria are separate; Sc&R, and A&J proxalaria are fused. The anterior axillary plate is composed of PC and C axalaria and fulcalaria (four sclerites), which are fused anteriorly and ventrally with ventral sclerites, the basalaria. The posterior axillary plate consists of Sc through J axalaria, fucalaria, and basivenalia (18 sclerites). PC&C basivenale ("humeral plate") is separate. In Ephemeroptera, columns are undulated but still aligned. The axillary plate is identical to that in Paleodictyoptera. Paleozoic Protodonata and Ephemeroptera (work in preparation) are morphologically between Paleodictyoptera and modern orders. Original drawing.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mented through excellent new material from Lower Permian strata of the Urals (104 specimens) and from Upper Carboniferous strata of Illinois (20 specimens), in addition to about 300 specimens from Moravia and Kansas that I know of previously. (Unfortunately, most of the material is still in my files, unnamed and unpublished.) The articular region in both the Diaphanopterodea and Paleodictyoptera is similar, but in diaphanopterids there is no fused axillary plate. In one partly folded wing I examined (*Permohymen schucherti*, No. 3815, Museum of Comparative Zoology, Cambridge), there is a long, V-shaped membranous gap between the anal and jugal rows of sclerites. Apparently, this gap folded when the wing was pulled back. There is no trace of a composite turning sclerite, equivalent to 3Ax of Neoptera. Because the "wing-folding" muscle is plesiomorphic, it probably folded the diaphanopterid wings, perhaps with several branches. These were attached to individual sclerites which were hinged to each other, not to one turning 3Ax.

The articulation of neopterans was also derived from the band of multiple, orginally hinged sclerites through fusion of sclerites into clusters called axillaria (singular axillary). However, the turning–pivoting cluster (third axillary, 3Ax) was formed as a specialization for folding the wings on the back; this and the other two clusters (first axillary, 1Ax; second axillary, 2Ax) had a different composition than the clusters of Paleoptera, the axilary plates. Note that the so-called "1Ax" and "2Ax" of Ephemeroptera are not clusters but single sclerites, namely radial proxalare and medial axalare (Figs. 16C, 16F), as will be fully documented later. Development of neopterous flight took a different evolutionary route involving indirect flight muscles. The turning–pivoting axillary 3Ax needed maneuvering space to execute its wing folding movement, and this resulted in development of a membranized gap at the cubital level interrupting the ancestral band of neopterous sclerites.

The pivoting and turning function of the neopteran third axillary is highly specialized. It brings the wings into the safely locked backward position, in which muscle tension is eliminated. This quality alone must have given neopterans a remarkable survival advantage.

The clusters of sclerites in modern Neoptera (axillaria) and Paleoptera (axillary plates) hardly show any sutural lines. At best, the original sclerites stand out as indistinct "bumps" connected by shallow grooves. However, fossil paleopterans often have a complete set of sharply delimited sclerites in the axillary plate (Kukalová-Peck and Richardson 1983, Figs. 3–5, 18); the oldest homoiopterid *Ostrava nigra* (Kukalová 1960) (see Kukalová-Peck and Richardson 1983, Fig. 20; Figs. 22, 24). In this way and others, Paleozoic insects give important clues on how the enigmatic modern articulation evolved.

In summary, a wing-folding ability occurs only when all wing veins are hinged to basivenalia and (or) fulcalaria and axalaria. This condition is present in Diaphanopterodea and in Neoptera. Since wings evolved from movable appendages and not from fixed, immobile tergal lobes (Kukalová-Peck 1978), wings with hinged veins are likely to be plesiotypic. Soaring and gliding in members of some paleopterous orders probably evolved as an adaptation for lower energy expenditure and may have happened several times. It requires simple linear fusions between several sclerites to form an axillary plate and another fusion with the axial wing veins (usually only R+). The wing-folding muscle in Neoptera is inserted on 3Ax, which is a composite cluster composed of some anojugal and cubital sclerites. An identical plesiomorphic muscle is present also in Paleoptera, in which it does (in Diaphanopterodea) or does not (in Paleodictyoptera, Megasecoptera, Permothermistida, Ephemeroptera, and Odonatoidea) fold the wings. The "wing folding" muscle was probably originally inserted mainly into the cubital fulcalare. However, the cubital fulcalare in diaphanopterids is a single sclerite, but in gliding Paleoptera it is fused, or at least rigidly hinged, into the cluster called the axillary plate. This cluster differs in composition from 3Ax of Neoptera because it is composed of subcostal through jugal basivenalia and fulcalaria in Paleodictyoptera, Megasecoptera, and Ephemeroptera and probably subcostal through jugal basivenalia, fulcalaria, and axalaria in Odonatoidea.

This morphological comparison shows that the muscle to the cubital fulcalare is plesiomorphic in Pterygota but, at the same time, it does not provide proof that the 3Ax of Neoptera is homologous to any sclerite of Paleoptera (see Hamilton 1972 and Rasnitsyn 1981 for an opposite view).

Pterothorax, tergal sulci, and symmetry

The pterothorax of homoiopterids was apparently about as long as high (i.e., relatively very high), and wider than long, as documented by the metatergum and the pleuron preserved next to each other (Kukalová-Peck and Richardson 1983, Fig. 1). Compared with this, the thorax of Recent odonates is also very high, but much narrower. Given their wing shape, paleodictyopterids must have been swift fliers (Wootton 1976), in spite of their primitive musculature. Recent dragonflies that use almost only direct musculature are difficult to catch in flight. Even Recent mayflies, which use a mixture of mostly direct and some indirect flight muscles, can be excellent fliers, i.e., the notoriously nimble Australian *Mirawara aapta* (E. F. Riek, personal communication).

As discussed by Boudreaux (1979), the pattern of occurrence of direct and indirect flight musculature in modern insects indicates that the mixture of both is plesiomorphic for pterygotes, while prevalently direct or indirect musculature is apomorphic. The flexibility of the thorax is expressed by the presence of sulci.

Tergal sulci in modern insects contain resilin, move slightly differentially during flight, and reflect to a certain degree the arrangement of thoracic muscles (E. L. Smith, personal communication). In homoiopterids, the sulci and all other flight connected structures are more numerous, more serial, and more regular than those in modern insects.

The terga of Paleodictyoptera were probably quite flexible with numerous bulges, as they are in modern Neoptera, and capable of upward deformation by means of indirect muscles (Figs. 16A, 16D). The presence of rather serially arranged muscles is documented by Kukalová-Peck and Richardson (1983, Figs. 1, 2, 7, 11). Simultaneous occurrence of flexible terga of nearly ground-plan articulation and venation strongly supports the presumption that flight was originally promoted by both direct and indirect musculature. Therefore, neither direct musculature of Odonata, nor direct and indirect musculature of Ephemeroptera means that either order is closer to Neoptera. In Neoptera, some primitive orders, namely blattoids (Blatodea, Isoptera, Grylloblattodea, Mantodea), primitive Paraneoptera including Zoraptera, and primitive Endopterygota (Coleoptera) evolved progressively towards the use of direct musculature (Boudreaux 1979). However, this phenomenon must be a convergent specialization because of the "mixed" ancestral state preserved in Paleodictyoptera.

Most regular and serially arranged are the sulci in nymphs (Fig. 23). In adults (Figs. 15, 16A, 16D), the central sulci at radial and medial levels are weakly pronounced, rather irregularily undulating, and apparently on their way towards being eliminated. All anterior sulci, especially at precostal, costal, and subcostal levels, and the posterior sulci are well expressed. In the lateral parts of the thorax occur short longitudinal sulci. Several (three or more) are aligned with the precostal, costal, subcostal, and radial rows of sclerites, while there is only one longitudinal tergal sulcus aligned with the medial, cubital, anal, and jugal rows.

The most laterally located tergites delimited by two transverse and one longitudinal sulcus, are here called "lobes." The largest lobe protruding into the articular area is the radial–medial lobe, which corresponds to the "shoulders" of modern insects. The anal lobe is also large, carrying an inflated, oval muscle attachment. The cubital lobe carries one or two V-shaped notches. Two deply sunken scars mark the mesial end of the radial lobe in all homoiopterid pteroterga (Figs. 15, 16).

Tergal–alar hinges and symmetry

In the most primitive homoiopterid paleodictyopterans shown here, in Diaphanopterodea and Permothemistida, and very likely also in the unknown ancestral Pterygota, the tergal–alar hinges involved all tergal lobes and all rows of sclerites, and therefore the hinge line was almost continuous. On the wing side, the articular sclerites were close to each other and were distributed almost regularly, especially in nymphs (Figs. 16A, 16D, 22, 23). On the tergal side of the adults the hinge line was interrupted twice and divided into three major sections: (*i*) the anterior section including precostal through medial lobes of the scutum; (*ii*) the medial section flanked by two short notches including a single, small cubital lobe; and (*iii*) the posterior section including a large anal and a small jugal lobe (Figs. 15, 16A, 16D).

Clearly, the tergal–alar hinge area of Paleozoic Paleoptera was much less diversified and much more regularily built than that of Recent forms. Again, the condition seems to indicate that flight structures, which *must* be asymmetrical, evolved from a set of more symmetrical structures, from a nearly symmetrical appendage with a symmetrical articulation supporting a nonforward type of movement.

The original continuous articulation between all eight tergal lobes and all eight rows of alar sclerites is still present in Recent Paleoptera, but is well masked by fusions, dispersal, change in size, and general desclerotization of the sclerites, as will be documented later. There is a basic outstanding difference between paleopterans and neopterans in the continuity of the articular band. In the paleopterous ground plan, the sclerites are modified but not interrupted by a gap at the cubital level. The neopterous ground plan differs because there is a wide gap near the tergum replacing a sclerite at the cubital level. The gap in articulation is the well-known membranous "window" providing maneuvering space for the turning–pivoting third axiallary (3Ax). Presently, the "window" is explained in textbooks as follows. In Neoptera, the second axillary (interpreted as a single sclerite homologous in all pterygotes) moved away from the tergum (Hamilton 1972; Gillott 1980). This conclusion seems logical according to modern morphology but when seen in the perspective of time, it is incorrect. The second axillary of Neoptera is a composite supersclerite, while the supposedly homologous "second axillary" of modern Ephemeroptera is a single sclerite (medial axalare) (Figs. 16C, 16F). The most primitive known pterygote articulation, introduced in this paper (Fig. 16), shows that the early pterygote ground plan had completely adjacent sclerites, no equivalent to the neopterous 2Ax or to the membranous area in which sclerites could shift, and no distally protruding tergal lobe at the cubital level which could have disappeared. The evolutionary event as deduced from modern morphology is not possible when confronted with evidence of the ancestral morphology.

The new "articular band" hypothesis offers another explanation: articulation of both paleopterans *and* neopterans started from the same ancestral articular band and all sclerites stayed roughly in their original place. This condition, even if masked and somewhat modified, is still present in Recent Paleoptera. In Neoptera, part of the cubital row of sclerites, which were aligned with the notched cubital tergal lobe (an early evolutionarily active area in flight adaptation), became partly membranized. This probably created the original gap opening towards the tergum and must have occurred simultaneously with the turning–pivoting 3Ax. This assumption is essential, because the 3Ax could not have started functioning without the space for turning within the primitive band of adjacent sclerites.

As shown above, the tergal–alar hinge carries additional important distinctive character between Paleoptera and Neoptera; in Paleoptera, the articulation is continuous as a ground plan, but in Neoptera there is an incomplete gap near the tergum, which replaced part of the cubital row of sclerites. A further significant difference is that in Neoptera some proxalaria adjoined the tergum and form some of the so-called articular "processes" (description in preparation), while in Paleoptera "processes" are tergal lobes.

Symmetry in venation of modern and Paleozoic wings

One of the important phylogenetic facts introduced in this study is that the wing venation and the wing articular sclerites were primitively aligned. The breaking up of the pro-wing lobe into venation was probably accompanied by fissuring of the dorsal epicoxa into articular sclerites. These were fulfilling two roles: holding the blood channels open (as they still do in modern insects) and serving as insertion plates for multiple primitive muscles (see previous text). The alignment must have provided free blood flow between the wing and the body (Kukalová-Peck and Richardson 1983; Figs. 15, 16A, 16D).

The veinal pair and the respective adjacent basivenale in modern insects shares the same original blood channel and therefore represent a phylogenetic unit, which always has to be considered together. The homologous venational nomenclature must, of necessity, reflect this relation, even if a vein happens to be cut off its own basivenale by a secondary flight fold. In some hind wings of Neoptera, parts of the anterior anal sector (AA) are cut off from the anal basivenale by folds (Wootton 1979, Fig. 11) and sometimes were erroneously not recognized as anals; they were called an "epusal" vein (Hamilton 1971, 1972) or even "postcubitus" (Snodgrass 1935). The identification error has been explained and corrected several times since (Carpenter 1966; Kukalová-Peck 1978; Wootton 1979; Boudreaux 1979), but faulty terms can have a long life. Later discussion will show that "epusal" vein and "postcubitus" are not simple terminological options for 1A as previously anticipated, but typological, nonhomologous terms for any branch of the AA bundle which came to be posterior to CuP.

Modern insects have a long history of wing adaptation towards a more "perfect" aerodynamic state, which has made the wing more and more asymmetrical and its venation more simplified. The changes were especially concerned with (*i*) the strengthening of the anterior wing margin by shifting the veins anteriorly; (*ii*) the building of the strong, parallel, axial supporting veins (R+, ScP−); (*iii*) the strengthening of the wing obliquely by several braces; (*iv*) the forming of a pliable, fanlike anal area, especially in the hind wing; (*v*) the forming of asymmetrical folds for deformation of wings during flight; and (*vi*) the loss of many branches (Fig. 15). Discussion here is necessary to show that in modern insects, there is an underlying symmetrical pattern of venation (Fig. 13).

Because of adaptive pressures towards asymmetry, veins of modern insects appear to be grouped into three types: simple veins (costa, subcosta); stemmed veins with branched convex (+) and concave (−) sectors (radius, media, cubitus); and stemless isolated branches arranged in a fan (anal, jugal). The radial stem is always convex, the medial stem is convex, neutral, or concave, and the cubital stem is convex, concave, or missing. There is a disagreement whether the concave sectors are principally the branch of the vein and the convex sector the actual vein (Lameere 1922) or vice versa (see Boudreaux 1979 and Hennig 1981 for discussion).

Similar analysis of venation in Paleozoic insects with emphasis on plesiomorphic features gives very different results (Fig. 15). (*i*) All primary veins demonstrate themselves as originally composed of a pair of dichotomously branched, primitively equal and, towards both margins, increasingly subequal sectors (Figs. 13–15). (*ii*) Veinal stems of veins R, M, and Cu are secondary and originated by fusion of two sectoral stems starting from a single basivenale. (*iii*) Originally, both sectors in a veinal pair were about equal, but later one prevailed over the other. (*iv*) Mild, regular fluting of sectors is as old, or almost as old, as the venation itself but the basal veinal stems in flying wings are afflicted by a variable secondary fluting (see following section) (Kukalová-Peck and Richardson 1983, Figs. 3, 4). (*v*) No braces, including the most common brace M-Cu, are primary, because they are absent from almost all Paledictyoptera (Kukalová-Peck 1969, 1970) and from some primitive Neoptera (Kukalová 1963, in opposition to Sharov 1966; Rohdendorf and Rasnitsyn 1980; Rasnitsyn 1980). (*vi*) Mild, regular fluting of the wing membrane is primitive and was primitively supported by the archedictyon (Kukalová-Peck and Richardson, Figs.

3, 4). (*vii*) Secondary venational elements such as intercalar veins, branches, the spurious vein of syrphids, intercalary supplements of odonates, bars, cross veins, secondary meshwork, and secondary archedictyon can appear any time and repeatedly in any evolutionary lineage and have a single source of origin, the archedictyon of Paleozoic ancestors.

Veinal characters occurring in the oldest and most primitive known insect wings are only seemingly different from modern insects. In fact, they still occur, but are scattered in various orders. They are most helpful for identification of homologous veins among pterygotes.

Precosta (Fig. 15)

The precosta (PC) in almost all modern wings is incorporated into the costal margin, because of its importance for pronation. The precosta was originally a veinal pair (as all other veins). The best evidence for this is the fact that in all Paleozoic Paleoptera a special row of precostal sclerites runs between the costal margin and the tergum, showing that there was a precostal blood channel. In homoiopterid Paleodictyoptera, PC sclerites are all fused with C sclerites (Fig. 16A, D), and are separated only by sutures. However, in Paleozoic and less distinctly in modern Ephemeroptera, the precostal and costal proxalaria are free from the precostal and costal axalaria (Fig. 16C, F). In modern Ephemeroptera and Odonata (Figs. 16B, 16C, 16E, 16F) basalar (= ventral) sclerites are articulated or fused to the precostal (but not costal) sclerites. All these features indicate that the precosta was primitively a regular veinal pair with its own blood channel opening into the body cavity (Figs. 13, 15).

In the elytron of modern Coleoptera there are two parallel ridges, one higher and one lower, called the "epipleuron." The epipleuron primitively seals the elytra against the body to protect the spiracles from dessication. Very probably, this structure represents the precostal pair in an original, fluted position. It appears that PC was "saved" from loss by acquiring the new sealing function. It should be noted that the alternative explanation of the epipleuron as a nonhomologous "new" structure is unlikely if we presume that wings are monophyletic.

Specialized (simplified) venation in the hind wing of modern Coleoptera is similar to the likewise specialized and simplified hind wing venation of modern Megaloptera. This similarity is caused by a parallel reduction of veins and cannot be primary (in contrast to Hamilton 1971, 1972). Coleoptera are much more likely to be the sister group of the neuropteroid stem group as mentioned by Lawrence and Newton (1982) and separated very early indeed, but before the veins became crowded and fused into the unified costal margin. This and other features in venation indicate that pterygotes radiated early, probably already at the late pro-wing stage.

Short epipleuronlike structures and a residual precostal vein can sometimes be detected in the forewings of fossil Homoptera (in preparation). Undoubtedly, a very early and unusual specialization of the forewing was responsible for preservation of PC in Coleoptera and Homoptera. The precostal pair could not have persisted in the flying wing of the usual membranous type, since crowding of the veins along the costal margin required the incorporation of PC (see Kukalová-Peck 1978 for references). Most Paleozoic flying wings have a serrated margin, which probably represents two fused precostal sectors with a series of little precostal twigs transformed into spines (Kukalová-Peck 1971, Fig. 2A; Fig. 3). Plesiomorphic symmetrical pro-wing characters are so irregularly scattered in modern insect wings and so variedly expressed that each group must have evolved separately from pro-wing to the modern form.

Costa

The costa in membranous wings is fused with the precosta and is the major vein supporting the costal margin. The complete phylogenetic formula of the pterygote costal margin is PC+, PC−, CA+, CP−, and SCA+ (Figs. 15, 18). A transverse cut across the anterior margin of a modern odonatan wing (Fig. 18) shows the complex nature of the anterior margin. In Paleodictyoptera (Figs. 16A, 16D), Ephemeroptera (Fig. 3), in Protodonata (in my file) and in the oldest Neoptera, CA and CP start widely apart from the basivenale and sometimes fuse well distantly from the base (Kukalová-Peck and Richardson 1983; Figs. 17C, 18, 20). In modern Neoptera, CA and CP also start apart but fuse together almost immediately at the base (Figs. 17A, 17B). A free section of CP− is barely visible only in large neopterous wings as a short, membranized groove (i.e. in forewings of Megaloptera). An exceptionally well-developed CP− is present in the stem group of Paleozoic Homoptera, especially in Scytinopteroidea, in which CP is branched and arched towards Sc as a brace (see schematic representation of CP in Fig. 15). According to E. F. Riek (personal communication) this unusual structure might have been used for stridulation.

Subcosta

In Paleodictyopteroidea, Ephemeroptera, and Protodonata, as well as in primitive Neoptera, with the exception of the Homoptera stem-group, the subcostal sectors do not fuse basally into a veinal stem but diverge: ScA+ is directed obliquely anteriorly and joins the costal margin, while ScP− runs parallel to R as a support to this axial vein. Several examples of primitive, long ScA+, which sometimes join the costal margin well beyond the midwing, are shown in Kukalová-Peck and Richardson (1983). ScA+ in Ephemeroptera is arched and branched, and forms a brace (Fig. 3) similar to that of CP in the Scytinopteroid Homoptera (Fig. 15). This "costal" brace, which should correctly be called the subcostal brace, serves a special kind of flight, limited only to Ephemeroptera (Brodskii 1974). In modern Blattodea, the free section of ScA+ forms an obtuse oblique ridge basally in the costal area (Kukalová-Peck 1978, Fig. 26). ScA+ is also visible in Mantodea, Embiina, large Megaloptera (Fig. 17), some Neuroptera, and elsewhere.

The most conspicuous ScA+ is in primitive modern Orthoptera, in which it plays a new role: strengthening the flanks of the wings when folded over the abdomen. The orthopteroid ScA+ is currently misinterpreted for the "costa," the true costa for the nonhomologous "ambient vein," and the area between them for the nonhomologous "precostal area." It should be noted that the "precostal area" does not exist in the pterygotes, unless it means a precostal strip, serrate margin, or epipleuron.

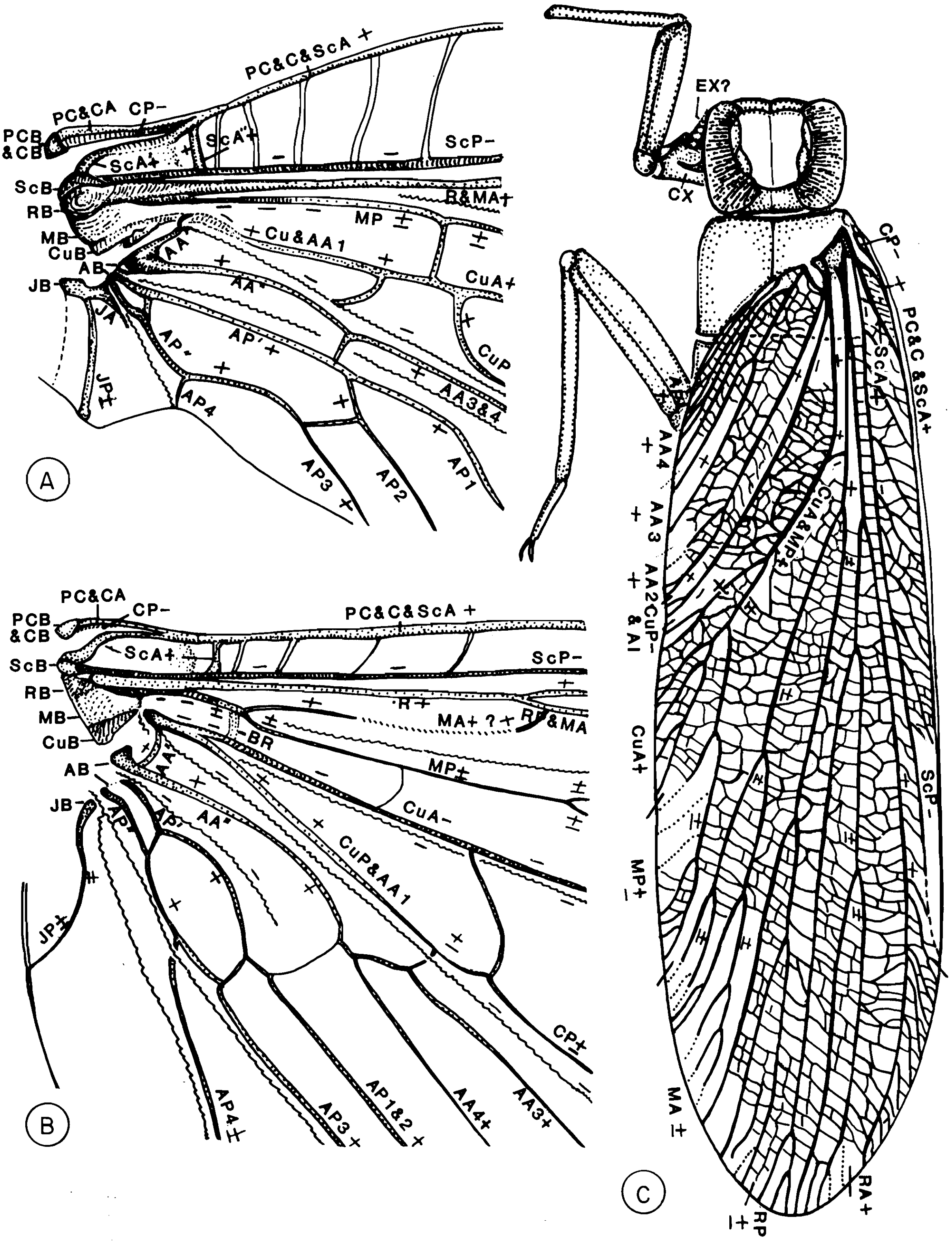
Some entomologists believe that the costa (+) and subcosta (−) together make a veinal pair and share a basivenale (i.e., Wootton 1979, Figs. 11, 12), but this is functionally impossible. The costal basivenale is hinged into the pronating unit (Fig. 15), while the subcostal basivenale is hinged or fused with a supersclerite 1Ax. The safest way to identify any vein is to follow it basally to its basivenale. This reveals that the orthopteroid "costa" starts from a wrong (subcostal) basivenale and is not in the pronating unit. If this old interpretation were correct, Orthoptera would have a special ground plan of articulation and would be a sister group of the Pterygota.

ScP− in Homoptera is unusual in that it is suppressed and tends to become fused with R. A section of ScP− near the base is clearly visible in the Paleozoic and Triassic stem group of Homoptera. Thus, in Scytinopteroidea, ScP−, is arched basally and forms a brace which is similar to CP− and ScA+ braces (Fig. 15) (for Russian scytinopteroids, D. E. Scerbakov (personal communication); figures of Australian scytinopteroids are in my documentary materials).

Radius

The radius almost always has a convex basal stem formed by a fusion of two radial sectoral stems. In flying wings, R serves as an axial vein and is always strong and convex. In primitive Paleodictyoptera, RA and RP are adjacent to each other (Carpenter 1943; Kukalová-Peck and Richardson 1983, Figs. 14, 17, 20), or they may be only partly fused (Kukalová-Peck and Richardson 1983, Fig. 18). In Paleozoic Permothemistida, RA and RP stems are not fused together but adjacent in *Lithoneura* (Carpenter 1943; and my files) and they become incompletely superimposed in *Protereisma* (Fig. 3). In all Protodonata and Odonata, RA and RP are never superimposed, but are separated or adjacent; the RP changed in the Namurian Epoch from an originally concave position to a secondarily convex one so that the change is actually recorded (E. F. Riek, in preparation; and figures in my files). In the Neoptera, RA and RP are fused together. Often they are also joined basally by media (M). RA, RP, and M fusion at the base might be connected with the wing folding, because it occurs also in the distinctly paleopterous but wing-folding Diaphanopterodea (Kukalová-Peck 1974). Odonate venation is similar to homoiopterid Paleodictyoptera (Kukalová-Peck and Richardson 1983), especially the oldest known dragonflies from Namurian strata of Argentina (E. F. Riek, in preparation). From the

FIG. 17. (A and B). Megaloptera (Corydalidae), fore and hing wing, showing remnants of plesiomorphic, more symmetrical ancestral venation, like PC−, ScA+, JA± and JP±. ScA+ starts distinctly from the subcostal basivenale and is similar to ephemerid subcostal brace (see Fig. 3). Note prominent AA′ and JA′ braces in the fore wing. AA_2, which in some fossil and modern plecopteroids and blattoids follows the claval fold distally, is suppressed. AA′ dividing into AA_1 (and AA_2), as well as AA″ dividing into AA_3 and AA_4, start as a bundle from an anal, not a cubital basivenale, and are therefore anal veins (not a "postcubitus" or an "epusal vein"). CuA and CuP are fused into a cubital veinal stem near the base and start from the cubital basivenale (CuB). Secondary changes in fluting are conspicuous: in the fore wing, M starts as a convex stem, immediately changing into a concave sectoral stem of MP, which soon becomes secondarily levelled to a neutral position. CuP starts secondarily as a convex vein, while the functionally necessary concave groove is formed by a secondary fold, etc. In the hind wing, CuA is brought down into a concave position by a fold, AP branches are secondarily convex, etc. Some of these changes are apomorphic for neuropteroid complex. Original drawing. (C) A representative of Neoptera, Paoliidae, erroneously considered ancestral to all pterygotes by the Russian school. The wings at rest were supposedly oriented obliquely backwards and supposedly gave rise both to laterally oriented wings of Paleoptera, and to posteriorly folded wings of Neoptera. However, the specimen figured here shows a typically neopterous wing folding and a plecopteroid type of venation. In paoliid venation, concave section of MP− bracing towards CuA is currently misinterpreted by Russian entomologists as "M5," a supposedly nonsymmetrical fifth branch of M. In fact, MP− fuses with CuA+ and separates from it again as MP±, while plesiomorphic MA± is richly branched. Note the well-developed CP− and long, strongly convex ScA+ starting from the subcostal vasivenale. *Protoblattina bouvieri* Meunier (1909, Plate V, Fig. 7). Muséum d'Histoire Naturelle, Paris, Upper Carboniferous (Stephanian), France. Drawn from the holotype; fore wing, length 28 mm; left fore wing omitted, angles of leg segments altered. Original drawing.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PC&CA
CP-
PCB &CB
ScA+
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ScP-
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RB
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CuB
+Cu&AA1
AB
AA'
JB
AA''
CuA+
JA
AP''
AP'+
CuP
JP±
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AA3&4
AP3
AP2
AP1
A
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CP-
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CuP&AA1
JP±
CP±
AP4±
AP3+
AP1&2+
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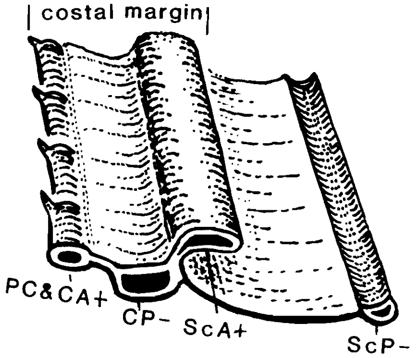

FIG. 18. Modern Odonata, basal transverse section through the costal wing margin showing its composition of serrate precosta fused with costa anterior (PC and CA+), costa posterior (CP−), and subcosta anterior (ScA+), forming an overhang. Anisoptera, Petaluridae, *Uropetala carovei* (White), New Zealand. Original drawing.

Paleozoic Ephemeroptera (Fig. 3), the early odonate venation differs in parallel arrangement of veinal stems with angular veinal crossings between them, but the veinal pattern is basically identical. Incorrect interpretation, stemming from poor knowledge of venational phylogeny (the radius was believed to be a single vein and, therefore, RP was interpreted as M), caused a chain of misconceptions in odonate venation which ultimately resulted in the presumption that the wing originated several times (Lemche 1940; Smart (discussion) in Wigglesworth 1963; Matsuda 1970, 1981; La Greca 1980).

Media

The two sectors of the media are usually fused into a veinal stem near the base. In Paleodictyoptera, Ephemeroptera, and Odonata, the stem of M is always separated from R (Kukalová-Peck and Richardson 1983; Fig. 16). In Odonata, M fuses with Cu (Figs. 16B, 16E), but in Neoptera and Diaphanopterodea, M is almost always either adjacent or fused with R. M sectors have variable fluting and are sometimes difficult to homologize (Carpenter 1966; Kukalová-Peck 1978). However, in many primitive Paleozoic Neoptera and some modern Neoptera, MA is mildly convex and MP mildly concave as a plesiomorphy.

Medial braces have lately caused some confusion in venational theory. MA, or anterior branch of MA, are often braced with the (posterior) radius, and MP with the cubital vein. The M-Cu brace is almost always present, because it is essential for most wings in flight. Yet this brace is secondary and is absent from almost all Paleodictyoptera (Kukalová-Peck 1969, 1970) and some primitive Neopetra (i.e., from many Paleozoic Liomopteridae of the plecopteroid stem group (Kukalová 1963). The hypothesis that M-Cu brace is primitively present in Pterygota was offered by Sharov (1964) and further developed by Rohdendorf and Rasnitsyn (1980) and Rasnitsyn (1980). The latter authors concluded that the media, in addition to four regular dichotomous branches 1, 2, 3, 4, sends off basally an asymmetrical branch "M_5." This conclusion is based upon erroneous identification of venation in the ancient Neoptera Paoliidae, which probably belong to the plecopteroid stem group (Fig. 17C). The "M_5" is a concave brace section of MP which fuses with CuA+ and separates from it again while showing neutral fluting, so that MP branches can be well recognized from convex CuA branches; the MA is richly branched and levelled. As shown in Fig. 17C, the Paoliid venation and fluting pattern is quite close to primitive modern Plecoptera; the richly dichotomous, archedictyon-filled branching reminds one of paleodictyopteran wings because of symplesiomorphy but not because of closer relation. The MA is so richly branched that it was considered by Russian authors as the entire M, which is inconsistent with the above-mentioned fluting present in all well preserved specimens[9]: Paoliidae are so primitive that the anal area in the hind wing was still relatively small and the hind wing folded probably only along the jugal fold, like in modern Endopterygota (undoubtedly as a symplesiomorphy) (Fig. 17C).

Henning (1981) recognized the secondary quality of M-Cu brace but did not see how varied it can be in different pterygote groups. There are at least six ways I know in which M-Cu brace may be formed: (*i*) by a section of CuA arched towards M (i.e., in some Homoptera and Diaphanopterodea); (*ii*) by MP arched towards CuA (in Plecoptera); (*iii*) by CuA fusing with M basally, separating from M and meeting concave $CuP_{1\&2}$ separated from $CuP_{3\&4}$ (in some fossil Cacurgidae (Protorthoptera); (*iv*) by a true cross vein between CuA and M (in some Homoptera); (*v*) by fusion between M and Cu (in Odonata); and (*vi*) by CuA arched towards M and touching it shortly (i.e., in Paleozoic Ephemeroptera, Fig. 3). Carpenter (1966) analyzed the media, its fluting and braces, and elucidated numerous phylo-

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[9] I revised paoliids in 1958 and studied almost all available specimens. The awkward fluting in the paoliid wing *Zdenekia* cf. *grandis* Kukalová, 1958 (Fig. 2), mentioned by Rasnitsyn (1981), is an artifact because the wing split between the membranes. Paoliidae (Fig. 17C) are plesiomorphic Neoptera probably with plecopteroid relationship, not common ancestors of Paleoptera and Neoptera, as the Russian school of paleoentomology interprets them (Kukalová-Peck 1978; Wootton 1981*a*). As shown in the specimen with a preserved body (Fig. 17C), Paoliidae folded their wings like other Neoptera and not halfway between Paleoptera and Neoptera (obliquely backwards), as suggested by Sharov (1966).

genetic aspects. Fluting of M was also discussed by Kukalová-Peck (1978) and by Wootton (1979).

Cubitus

In Paleozoic insects, as far as I know, the cubital sectors are always basally fused, but the veinal stem is short. In modern insects, such as some Orthoptera, Homoptera, and Endopterygota, the cubital sectors may not be fused basally. In Paleodictyoptera, cubital sectors are present in the near original state and are both dichotomously branched in primitive forms (Kukalová-Peck and Richardson 1983). In advanced modern insects, the cubital region is very active in flight, especially along the CuP, and considerable change in fluting (Fig. 17B) and from the original, symmetrical Cu takes place. In almost all insects, with the exception of Paleodictyoptera, there is an AA brace between CuP and the rest of AA, which is often dissected by a secondary fold. The brace is formed by the anterior branch of AA and is usually inconspicuous (Figs. 17A, 17B).

Anal

In some Paleozoic insects, especially in Paleodictyoptera (Kukalová-Peck and Richardson 1983) and Protodonata (unpublished figures), anal veins still show their original, short sectoral stems, starting separately from the anal basivenale. This primitive condition demonstrates that the anal vein should be viewed and treated as homologous to the other venation, and not as a fan of several asymmetrical veins without broader homologues. There are, in fact, only two anal sectors which are branched in a predictable way.[10] Other supporting evidence that the anal vein is comparable to all others is the fact that it has its own row of anal sclerites (Figs. 16A, 16D). Successive numberings of anals is a simplification and does not reflect correctly the phylogenetic relations in the anal area. In many primitive modern insects, anals are distinctly grouped into two bundles (Fig. 17A), which is the next primitive stage after the sectoral stems became reduced. The AA bundle is often separated from the AP bundle by the anal fold, but this feature is not always present and may be variably expressed (Wootton 1979).

The anal area must be braced against buckling during flight (Kukalová-Peck 1978). Paleodictyoptera evolved a special, barlike secondary brace which transversely crosses anal veins near the base (Kukalová-Peck and Richardson 1983, Figs. 3, 4). All other pterygote orders use the upper parts of stems of anal branches to build up a brace between anal basivenale and CuP (Figs. 3, 16, 17). Distally, the AA bundle sends off a branch (probably most often AA_1) (Fig. 17) which fuses with CuP or, seldomly, runs parallel to CuP (Hamilton 1971, 1972, Part III, Figs. 10, 16). The AA-CuP brace may be interrupted by claval and anal folds (Wootton 1979, Fig. 11; Figs. 17A, 17B).

Both AA and AP bundles are originally dichotomously branched (Figs. 3, 15). Since flight adaptation happened in parallel, the part of AA proximally from fusion of AA_1 with CuP is different depending on the order, the richness of the venation, and whether it is the fore or the hind wing (Kukalová-Peck 1978, Fig. 26). In modern Neoptera, the free AA may be represented by AA_2, AA_3, and AA_4 branches as in recent primitive Plecoptera from Australia. However, the AA bundle is usually reduced and, if a single vein is present, it is often $A_{3\&4}$, while A_2 is missing (Figs. 17A, 17B).

In the last 30 years, the existence of two original sectors within the anal vein have been subconsciously anticipated, but the concept was put forward in an erroneous way: part of the sector AA, which sometimes becomes cut off from its basivenale by a fold, has been interpreted as a single vein starting from the cubital basivenale (Snodgrass 1935; Hamilton 1971, 1972). This seemingly single vein was named the "postcubitus" and "epusal" vein. The error has been discussed in more detail earlier, but perhaps it should be noted that the example of AA shows, explicitly, how important one's phylogenetic attitude is for identifying venation. This is a well-known fact at the specific and generic level. However, it is not less valid even at the highest systematic levels. Errors in the basic ground-plan venational model directly influences venation identification on specific levels. Venation radiated so early that even extremely plesiomorphic veinal features, such as a richly branched AA, may be present in the modern fauna and may confuse comparisons, because these are habitually based upon a reduced, derived (and incorrect) venational model. The anal veins will provide much better information for cladistic analysis if they could be better homologized. This will not come easily, but it is not an impossible task.

Homologous terms for wing venation (here used with adjustment for the paired nature of all veins) have been used for a long time, are generally known, massively documented, and well established in the literature (e.g., see Riek 1970 in *Insects of Australia*). They form a solid base for cladistic analysis. Aberrant, additional, and order "specific" terms such as "postcubitus" are not only unnecessary, but misleading because they mark the veins as unique entities without evolutionary ties to basivenalia. In contrast, homologous veinal terms clearly show which vein and which basivenale form an evolutionary unit, based upon an ancient blood duct. This knowledge is pivotal in homologizing pterygote

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[10] Additional, alternating concave veins in the anal area of Permothemistida (= Archodonata) mentioned by Rasnitsyn (1981, Fig. 10) as possibly primitive for pterygote venation are intercalated veins which are secondary (my personal observations in 1981 of original material).

venation. Unusual terms for primary veins such as postcubitus and empusal vein for some part of AA and plical vein for CuP should therefore be avoided. Successive numbering of anal sectors, presenting primary veinal braces as cross veins, etc., hide inadequately researched veinal characters from the attention of specialists and from ultimate homologization. It is better to mark an uncertain vein with the most likely homologous term and a question mark than to call it by a different term and to circumvent homologization. With the methods, needs, and merits of cladistic analysis in mind, inadequately homologized characters are either almost useless or deceptive because their plesiomorphic–apomorphic evaluation is then a random guess.

Jugal

The jugal area, called "neala," was a character upon which Martynov (1924) divided Neoptera. Absence of neala characterized Paleoptera. However, the jugal area was recently found also in the Paleoptera, in Carboniferous Paleodictyoptera, the Homoiopteridae (Kukalová-Peck and Richardson 1983, Figs. 3–5). Therefore, the jugal area is primitive for all Pterygota. In those Paleoptera which do not show its presence, it is secondarily reduced. I found that in large, primitive modern Ephemeroptera such as Siphlonuridae, the jugal area is still noticeable and that there is also a remnant of a jugal row of sclerites separate from the anal row of sclerites (Figs. 16C and 16F, oblique striations); these features stand out after the specimen has been tinted with fuchsin.

Jugal veins in Paleodictyoptera are variable, more or less reduced in branching, and obviously represent a receding structure. However, they often are preserved well enough to show that the jugal pair was originally symmetrical to all other wing veins. This fact finds strong support in the row of jugal articular sclerites found in Paleodictyoptera, Paleozoic Protodonata, Odonata, and Ephemeroptera. The jugal row is either fused with the anal row or separated (Fig. 16). Mildly fluted and short-stemmed jugal veins occur rarely in Paleodictyoptera and in Paleozoic Ephemeroptera (Fig. 3); simple, distinctly fluted jugal veins are found in Paleozoic Protodonata (in preparation).

Jugal veins in modern Neoptera are usually reduced, and their paired nature is obscured (Wootton 1979). Hamilton (1971, 1972) considered the jugal as a secondary bar; however, the jugal vein and its basivenale are present in some large specimens of modern primitive insects (Fig. 17A). The same figure shows that in the megalopterid forewing the jugal anterior JA crosses the jugal fold and fuses with AP, thus forming a brace. The posterior free jugal is therefore the sector JP, probably as in many other modern insects.

Original branching and fluting

The original number of dichotomous branching seems to be three or four, but might have been more in the symmetrical pro-wing. Primary branches must be distinguished from secondary intercalar veins.

Secondary branches might suddenly occur in the membrane at any systematic level especially if the wings become larger, to supplement venation. Intercalar veins, true cross veins, reticulum, transverse bars, veinal supplements, etc., do not have tracheae (however, primary veins sometimes also do not have tracheae, especially if they are reduced as C in Orthoptera).

The following types of fluting are present in the insect wing. Fluting in primary veins is formed by accumulating cuticle alternately on dorsal and ventral sides of the wing. Secondary changes were discussed by Carpenter (1966), Kukalová-Peck (1978), and Wootton (1979). The interveinal membrane is primitively fluted by the undulated archedictyon (Kukalová-Peck and Richardson 1983, Figs. 3, 4, 6). Flight-connected folds (medial, claval, anal, and jugal) (Fig. 15) were described recently by Wootton (1979) and are mostly quite variable. They occur along the primary veins in the membrane or cut across the stems and branches showing that they originated after the primary venation was established, during the flight adaptation, and separately in each lineage.

It should be noted that fluting in fossilized wings might sometimes be influenced by the vagaries of preservation. Any wing can be preserved in no less than six ways: as imprint and counterimprint of the dorsal side, as imprint and counterimprint of the ventral side, and as two opposite halves when the wing splits between the membranes. The last type of preservation is quite common, especially in heavily sclerotized, large wings, and it results in peculiar, mostly concave fluting because the split may expose the hollow inside of the veins (i.e., in a paoliid *Zdenekia grandis* Kukalová, 1958, Fig. 2, misinterpreted by Rasnitsyn 1981; compare with the well-preserved paoliid *Zdenekia grandis* Kukalová, 1958, Fig. 1, and with Fig. 17C here).

Changes of fluting in veinal stems

Veinal stems result mostly from the + sector being superimposed on the − sector, and should be, therefore, originally mildly convex. The stem of the radius is always convex in all pterygotes, because it serves its function as the major axial vein. However, the rest of the wing base varies in fluting according to the special requirements of flight. As a rule, the protruding R+ stem is flanked by two grooves: anteriorly by the parallel, receding ScP−; posteriorly the groove is broader and involves various veinal stems. In

Homoiopteridae and many other Paleodictyoptera, R+ is followed by two concave stems, M− and Cu−. In wing-folding insects, the stem of M becomes usually adjacent to R and is sloped, concave, levelled or convex. Other times, R+, M−, and Cu+ alternate, etc.

In the superimposed, fused veinal stems, the original + fluting can be changed to − by simple reduction of the superimposed convex sectoral stem. This reduction causes changes of fluting in the medial and cubital veinal stems. The anterior (convex, +) and posterior (concave, −) sectors separate at the end of the stem as if they were mere branches. However, in an evolutionary sense, the two main "branches" are the sectors themselves. It is therefore neither true that the convex sector is the "vein" and the concave sector the "branch" as anticipated by Lameere (1922), nor that concave sector is the "vein" and convex sector the "branch" (Boudreaux 1979). It should be kept in mind that in all stemmed veins both sectors of the primary venation are originally present in their full length, but parts of them are often fused with some other veins or suppressed, and the fluting has been alternated.

The pterygote pleuron, its origin and subdivisions

As expected in large, aerial insects, the pleuron of homoiopterids is high and strongly sclerotized (Kukalová-Peck and Richardson 1983, Figs. 1, 2). It is divided by an inflexion, the pleural sulcus, into an episternum and epimeron. The inflexion protrudes dorsally above the pleuron forming a knob, the ventral wing process (VWP), which serves as the central wing pivot. The VWP is flanked by the ventral wing sclerites, the basalaria (BA) and subalaria (SA), which are too faintly preserved for description. However, the ventral articular sclerites were probably similar to those of Paleozoic Diaphanopterodea, Ephemeroptera, and Protodonata, i.e., were multiple and more or less arranged into a band, interrupted by the VWP. Some modern insects also have several ventral sclerties, very likely because of a higher number of ventralia in the ancestral pterygote (i.e., two basalaria of Orthoptera, Trichoptera, Lepidoptera, some Diptera, and others and two or three subalaria of Ephemeroptera). Hinged fusions of basalaria with the episterum, which occur in some Neoptera (e.g. Megaloptera), are not present in fossil or modern Paleoptera and are in all probability secondary.

The homoiopterid pleuron (Kukalová-Peck and Richardson 1983, Figs. 1, 2) has shallow, bowlike ripples but is not subdivided into anapleurite and katapleurite. However, the katapleurite might have been broken off along the predisposed line of subdivision against the anapleurite.

Previously, I described "anapleuran" and "katapleuran" rings in a homoiopterid *Monsteropterum moravicum* (1972, Fig. 10), but that interpretation has been corrected after studying additional material. The "anapleuran" ring was the coxo-trochanteral intersegmental membrane, which became exposed when the legs were bent and the "katapleuran" ring was the trochanter (see Fig. 10 for correction). A very similar case of an exposed intersegmental membrane is published in an accompanying paper (Kukalová-Peck and Richardson 1983, Fig. 1). Homoiopterids probably needed very strong legs to stay perched while sucking on strobili, because their large wings acted like sails in gusts of wind. The error is typical for paleontological work, in which a superficial similarity to modern material can be very deceiving.

The most primitive pterygotes in almost all evolutionary aspects are Paleozoic Diaphanopterodea[11] (the sister group of Paleodictyoptera, Megasecoptera, and Permothemistida, capable of folding wings backwards by a simple mechanism). Their subcoxa (pleuron) is always well sclerotized and more or less crescent shaped (Fig. 1). The existence of a suture dividing the subcoxa into an anapleurite and a katapleurite is uncertain. The subcoxa is articulated dorsally by the membrane to basalaria and subalaria and ventrally to the coxa by a single condyle. The morphology of the diaphanopterid subcoxa is indicative of a leg segment that became embedded in the body wall and kept its proximal and distal articulation.

The dorsal and ventral wing articulation is interpreted here as derived from the first leg segment, the epicoxa, which became embedded in the body wall along with the second leg segment, the subcoxa. Hence, a minimum of two segments should occur above the coxa in euarthropodan and crustacean legs. In the primitive crustacean *Anaspides*, two segments were recognized above the coxa by Carpentier and Barlet (1959, p. 113), by Sharov (1966, p. 167), and by Hennig (1981, p. 92). The actual homologization between the pterygote leg and *Anaspides* leg is, nevertheless, unclear. Following the Carpentier and Barlet interpretation, the subcoxa is a precoxopodite, and the insect epicoxa (first segment) would be a laterotergite. Following the Sharov and Hennig view, the subcoxa is a coxopodite, and the epicoxa would be a precoxopodite. Obviously, the crucial problem is how the crustacean leg starts, with a laterotergite or with a precoxopodite. Unfortunately, the morphology of fossil pterygotes does not bring clues for solving the crustacean argument other than that the insect pleuron and wing articulation are best explained as derived from a minimum of two leg segments above the coxa.

One variant of leg interpretation promoted by Sharov (1966) presents the subcoxa as a fusion of two original

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[11] The references to Diaphanopterodea (= Eumegasecoptera) in Hennig (1969, 1981) are outdated.

euarthropodan segments, expressed primitively as an anapleurite and katapleurite. This possibility cannot be excluded, as far as fossil pterygotes are concerned. A very primitive Carboniferous protodonatan nymph has subdivided subcoxa (in preparation). If there was such a fusion, it must have happened already in mandibulate ancestors, before the Crustacea and Tracheata originated. However, subcostal subdivisions of the Tracheata are quite varied and may be interpreted with equal probability as secondary reinforcement or as subdivisions of a segment due to desclerotizations around muscle insertions. In comparative dissections of living arthropods, Smith did not find any proof that the subcoxa is composed of more than one segment (E. L. Smith, personal communication). Whatever the answer is, it should be sought in trilobitomorphs or other very primitive fossil arthropods which might still carry the plesiomorphic condition.

The sister group of Pterygota are Thysanuroidea, including extinct Monura and modern Thysanura (silverfish, excluding Archeognatha). As a background for this paper, I studied some Monura, namely part of the original collection of *Dasyleptus brongniarti* Sharov, 1957 (Lower Permian strata of southwestern Siberia), and a beautifully preserved specimen (No. P11E751) from the private collection of C. Cozart, Chicago (Upper Carboniferous of Mazon Creek, Illinois). A dicondylous mandible and the presence of gonangulum in the ovipositor document that Monura are true thysanuroids, in spite of their "machilid" appearance. Contrary to common belief based upon Sharov's description, I found Monura generally close to the basic dicondylate plan, probably representing a mildly apomorphic side branch of the thysanuroid stem group. A detailed revision of morphological features is in preparation by Carpenter (F. M. Carpenter, personal communication). The subcoxa of silverfish is desclerotized and the anapleurite, katapleurite, and pseudotrochantin[12] subdivisions stand out as crescents separated by a membrane (Boudreaux 1979). In contrast, Paleozoic Monura have a well-sclerotized, short subcoxa (Fig. 5) as was shown correctly by Sharov (1966, Fig. 33B). I was unable to detect the membranous strip above the subcoxa as anticipated by Boudreaux (1979) in the material available to me for study. The subcoxa seems to be directly articulated to the fused epicoxa and pro-wing lobe (see further text and Fig. 5).

The sister group of Dicondylia (Pterygota and Thysanuroidea) are Archeognatha[13], in which the subdivisions of the subcoxa are poorly expressed (Matsuda 1970). In modern Archeognatha, the subcoxa articulates dorsally at one point with the fused epicoxa and pro-wing and is not fully embedded in the body wall (E. L. Smith, personal communication). Barlet (1950) assumed that machilids have a special kind of subcoxae on meso- and meta-thorax, composed only of the katapleurite, while the anapleurite has joined the underside of the paranotal lobes (Manton 1977, Fig. 9.9; Boudreaux 1979). Here, a more simple interpretation can be offered: the machilid subcoxa is not exceptional, but similar to that of all other insects, and is a complete segment. The "additional" sclerite above the subcoxa is the ventral part of the epicoxa which corresponds to the basalaria and subalaria of the pterygota. The ventral part of epicoxa became fused under the pro-wing lobe because it was not functional but otherwise stayed in its original position.

There is a vast literature concerning the origin of the pleuron and the role of the subcoxa as the wall-reinforcing element. Detailed reviews have been offered recently by Sharov (1966), Matsuda (1970), and Boudreaux (1979). Sharov (1966, p. 187) believed that the pleuron was produced by two euarthropodan leg segments, represented in crustaceans by a precoxopodite and coxopodite. Matsuda and Boudreaux interpreted the subcoxa as a composite of the coxal fragment (katapleurite) and the secondary pleural sclerotization (anapleurite). It should be noted that in modern embryos the anapleurite is often membranous (Boudreaux 1979).

The view supported in this paper is based upon the outer morphology of fossils as well as on the broadly based comparative study of arthropods made by Smith which will be published in his upcoming book. The insectan subcoxa (= pleuron) is considered to be a single (second) segment of the euarthropodan leg which in Dicondylia became embedded in the body wall; the subcoxa articulated between the epicoxa and coxa and was primitively well sclerotized. Therefore, any desclerotization is bound to be secondary and any similarity of subdivisions is presumed to be convergent.

Subcostal subdivisions such as the katapleurite, anapleurite, less frequently the pseudotrochantin, and other subdivisions also occur in Myriapoda and

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[12] True trochantin is limited only to Neoptera as an apomorphic character, and is an episternal fragment (Boudreaux 1979, p. 176). The trochantin is primitively absent in all Paleoptera.

[13] Archeognatha differ from Dicondylia mainly (*i*) in the presence of primitively monocondylous jaw, (*ii*) in the lack of a gonangulum in the ovipositor, (*iii*) in a subcoxa incompletely embedded in the body wall, and, according to E. L. Smith (personal communication), (*iv*) in a different structure of the labrum. Gonangulum was discovered by Scudder (1960, 1964).

Endognatha (Manton 1977; Boudreaux 1979). They are expressed in various ways, sometimes as crescents widely separated by a membrane (Fig. 7), at other times as adjacent plates (Fig. 6) or as rings associated with the free limb (in Collembolla; Boudreaux 1979). It seems that in Tracheata the subcoxa became incorporated into the body wall in steps, and various stages of this process can be traced in several groups. This does not concern the Dicondylia, however, because they always have a fully embedded subcoxa.

In primitive, large Paleozoic Diplopoda, the subcoxa is incorporated and well sclerotized, as shown in Fig. 6, and the epicoxa is separated from the tergum by a suture. In modern Diplura, which are similar to ectognathous insects, sections of the subcoxa are sometimes interpreted as anapleurite, katapleurite, and pseudotrochantin and are also fully incorporated (Fig. 7), but quite differently in the thorax and in the abdomen. In Protura, the supposed anapleurite is fixed and the katapleurite is slightly mobile (Boudreaux 1979, p. 148). In Collembolla, only anapleurite is incorporated in the mesothorax, while *both* anapleurite and katapleurite are not incorporated but associated with the coxa in the metathorax (Boudreaux 1979, Fig. 67).

The relatively highly varied expression of the subcoxa in the tracheates seems to be best interpreted as follows. Tracheates probably inherited the epicoxa incorporated into the body wall, but the subcoxa was still free. The subcoxa remained free in the head appendages, but in the trunk it became gradually incorporated into the body wall, apparently parallely in all groups. In the process, the subcoxa sometimes became divided into subdivisions known as anapleurite, katapleurite, pseudotrochantin, and others, which may look similar in some groups and give the superficial impression of homology. However, this similarity is probably caused mostly by similar muscle insertions and similar reinforcements, and may be partly influenced by convergent movement of the limbs (Manton 1977). In Collembolla, the meso-katapleurite and meta-subcoxa remained associated with the coxa in the thoracic limbs, probably because this group is neotenic (Boudreaux 1979). Incomplete separation of the subcoxa from the coxa, in a neotenic animal, would not necessarily prove that these two limb parts originally belonged to a single segment, as anticipated by Boudreaux, but rather that the segment-forming process in the evaginated limb might have been halted before it was completed.

In the most primitive modern ectognathous insects, the Archeognatha, the incorporation of the subcoxa into the body wall is incomplete (E. L. Smith, personal communication), but it is always complete in the Dicondylia (Monura, Thysanura, and Pterygota). Undoubtedly, this feature is a basic, shared synapomorphy of the group and is directly connected with the origin of wings (the subcoxa provides the necessary area of muscle attachment and the central wing pivot). The fully sclerotized subcoxa is primitive for the Dicondylia, since it occurs in Monura as well as in the most primitive fossil Pterygota. Desclerotization of the subcoxa in modern Thysanura is a secondary autapomorphy, correlated with cryptic life, winglessness, elongate coxae and, in higher Thysanura, with a very specialized type of leg movement (Manton 1977; Boudreaux 1979).

Articulation in early pterygote nymphal wings

All modern nymphs have immobile wings and the wing articulation is either vestigial or reduced and smoothed out. They sometimes appear to be like the laterally extended, doubled tergal lobes (paraterga) of crustaceans, chelicerates, and trilobitomorphs. The only evidence of their past mobility may be the "flipping over" of the nymphal wings during late ontogeny in modern Odonata and Orthoptera (Kukalová-Peck 1978), the presence of a distinctive suture between the terga and wings in modern peloridiid nymphs (Evans 1939 and my personal observation), the "Paleozoic" position of nymphal wings in some Ephemeroptera (*Analetris* Edmunds 1972), occasional experimentally induced "throwback" articular structures in modern nymphs, and "bumpy" vestiges of articulation in primitive nymphs such as Plecoptera.

In contrast, many Paleozoic nymphs had more or less, or even fully, articulated wings that were partly or fully mobile and sometimes functional. There is direct evidence that primitive Pterygota had nymphs with articulated wings but that the articulation was lost during the Paleozoic or later (Kukalová-Peck 1978; Figs. 19–28).

Primitive articulation and mobility of nymphal wings and the "pleural appendage" theory of wing origin are two sides of the same coin. It is hard to imagine that the wings started as mobile structures, yet they were not originally present on nymphs as well as on adults (see Wootton 1981*a* for an opposite view). Once we accept the "pleural appendage" theory, the mobility of nymphal wings is not optional but inevitable. Further supporting evidence was found in the ontogeny of primitive modern insects, the wing buds of which are of pleural origin and evaginate from the pleural wall (Bocharova-Messner 1959, 1971; Tower 1903). Indirect but very important evidence is the absence of a metamorphic instar in representatives of those Paleozoic orders which had articulated nymphal wings (Kukalová-Peck 1978). The metamorphic instar was not yet needed because it is an adaptation evolved to *reconstitute the wing articulation*.

The fossil record on nymphal articulation and primitive mobility of nymphal wings in Paleozoic insects was recently challenged by Wootton (1981*a*).

He felt that the wings are probably pleural because of evidence in modern ontogeny and that my interpretation may ultimately prove to be correct, but that knowledge of the fossil record on some Paleoptera and most Neoptera is now too insufficient to be sure. But my conclusions were fully inspired by and based on fossil record, long before I searched (and found) supporting evidence in modern ontogeny. Further, a ground-plan plesiomorphic feature does not have to be found in several systematic units to become more "truthful." Surely, all we need as proof is a well-documented case of nymphal wing articulation either in Paleoptera or in Neoptera. However, it is comforting to know that the presently available fossil evidence is quite satisfactory (Kukalová 1968; Kukalová-Peck and Peck 1976; Kukalová-Peck 1978, p. 61) and the idea has the support of other specialists, e.g., Sharov 1957*a*, 1957*b*, 1966, 1971*a*, 1971*b*; Carpenter and Richardson 1968; Rasnitsyn 1981; and Sharov and Sinitshenkova 1977. A short summary follows.

Criteria for recognizing, in the fossil state, an articulated nymphal wing from a wing with vestigial and already nonfunctional articulation can be unclear, unless the wing is found preserved at an angle to the body. However, a neopteran nymph in this rarely preserved condition has been known for 25 years (Sharov 1957*b*, Fig. 3) and more specimens are awaiting publication (Kukalová-Peck 1978).

Very young nymphs cannot be expected to have articular sclerites well expressed because the whole body was very soft. On the other hand, some modern nymphs with perfectly immobile wings have "bumpy" vestiges of articulation which could be mistaken for a functional articulation if they were to become fossilized. Under these circumstances, the most reliable positive evidence for articulation in the fossil state is the massive occurrence of detached wing pads of various ontogenetic sizes belonging to one species, or at least to a closely related group of species. My observations and those of others have been that immobile, fused wing pads are usually shed with the tergum as one piece! In contrast, adult wings and articulated nymphal wings break off along the line of maximum weakness, which is in the articulation.

The pivotal evidence for articulated nymphal wings used by Kukalová-Peck (1978, p. 61) were over 100 detached wing pads of closely related Lower Permian nymphal protereismatoid Ephemeroptera. This number has now been increased to several hundred, and double that number were discarded in the field by Carpenter (1979, p. 270). The length of wing pads ranged from 2.8 mm to 7 mm, but most were in the vicinity of 5.5 mm (Carpenter 1979). Protereismatoids are believed to be directly ancestral to modern Ephemeroptera. However, their nymphal wing pads are not "tucked" away on the back as in living forms and fused with the terga, but are lateral, articulated, and probably mobile (Kukalová-Peck 1978, Figs. 28, 29, 30). They provide evidence for an evolutionary succession, in the most primitive of living pterygotes, from a condition with articulated lateral wings to one with fused wings in a more or less dorsal and completely afunctional position. It is remarkable that this transition happened relatively late and therefore is recorded in the fossil evidence.

Fossil evidence also shows that loss of the nymphal wing articulation had already occurred in the Paleozoic in blattodeans, homopterans, and probably in some other neopterans. There were also many Paleoptera in which the articulation was more or less present, but apparently not at all or little used, i.e. in Paleodictyoptera (Kukalová-Peck 1978; Wootton (1981*a*) overlooked most of this information, which led to his unfounded criticism). Changes in articulation had to be eventually compensated for by the metamorphic instar and this led to the independent origin of metamorphosis in several pterygote lineages (Kukalová-Peck 1978).

Neopterans seem inclined to loose their nymphal articulation more readily. However, the fossil record of articulated nymphal wing pads is fully sufficient to provide proof that neopteran nymphs *also* had primitively articulated wings. I have recently (1981) studied the largest collection of detached juvenile wings, deposited in the PIN, Moscow. An ancient protorthopteroid neopteran *Narkemia angustata* Mart. from Upper Carboniferous strata of the Tungusk basin is represented by about 60 wings, over 90% of them juvenile. The smallest nymphal wing is only 6 mm long (specimen 3115/270); young subimagos have wings ca. 22 mm long (specimen 3115/218) and most wings of subimagos are 33–38 mm long. The largest (probably adult) wing is 44 mm long. All juvenile wings had a thicker membrane, darker pigmentation, dense microtrichia, less expressed corrugation, and broader, less distinctly delimited wing veins. Another plentiful record of detached protorthopteroid juvenile wings is of *Atactophlebia termitoides* Mart. from Upper Permian

FIGS. 19–22. Specimen and interpretation of a young, primitive, paleodictyopterid nymph with well-developed articulation; wings were probably at least partly functional. The articular band is rising along an undulating line high above the tergum and sloping gently towards the wing. The mesotergum and articular band are posteriorly scalped. Paleodictyoptera, Homoiopteridae, *Adolarryia bairdi* Kukalová-Peck & Richardson, 1983, holotype; Upper Carboniferous, Illinois; fore wing, length 24 mm. Figs. 19 and 20, ammonium chloride coated obverse under different lighting; Fig. 21, close-up of uncoated obverse; Fig. 22, original drawing of interpretation.

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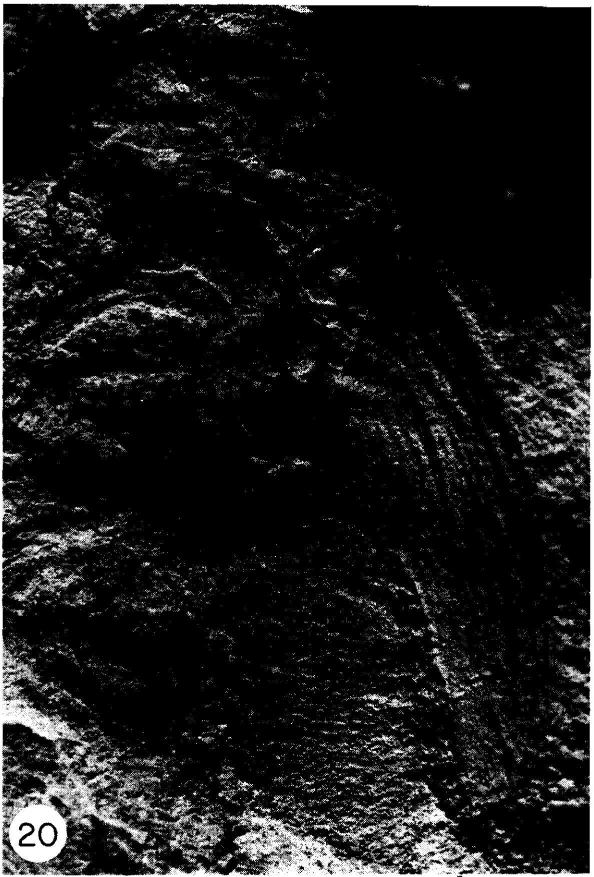

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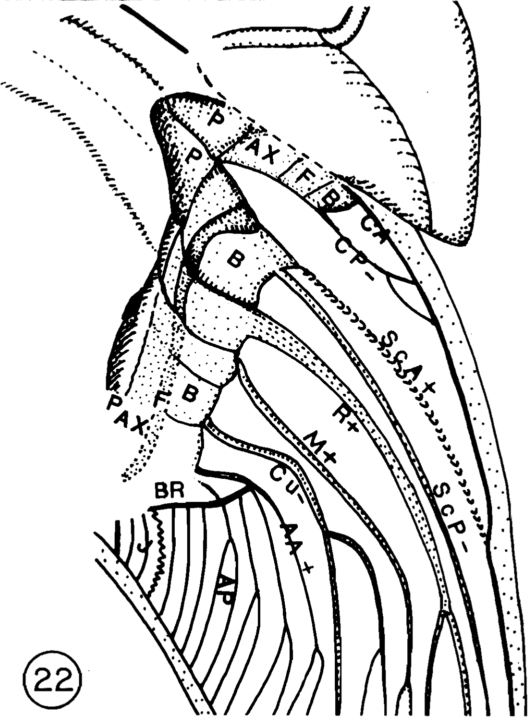

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strata of the Urals. There are about 40 specimens having an identical set of juvenile characters now present in the collection. The exact measurements of 17 specimens were published 25 years ago by Sharov (1957*a*), who recognized at least three groups, with wing lengths of 23–24 mm, 30–35 mm, and 40–43 mm. He interpreted them as flying nymphs. Additional evidence for articulated wings was published by Rasnitsyn (1981). (More material, some with bodies and small attached wings oriented to them at an angle, awaits publication.)

Thus, there can be no doubt, even with the limited documentation published so far, that juvenile Paleozoic Paleoptera and Neoptera had articulated and mobile wings and that Wootton's (1981*a*) concern about an insufficient record is unsubstantiated. The embryological, genetical, and physiological evidence against the paranotal theory is lately accumulating so rapidly that, in another 10 years, it might be hard to believe that it had been once considered a serious alternative to the pleural appendage theory.

Ontogenetic development of wing articulation in paleodictyopterid nymphs

Paleozoic and modern nymphs have many features that give clues to evolutionary events. A statement such as "nymphs are not ancestral pterygotes" (Wootton 1981*a*, p. 337) is a mere truism that has no bearing on evolutionary theory. The human fetus is also not an ancestral primate, yet, it is an invaluable source of evolutionary information.

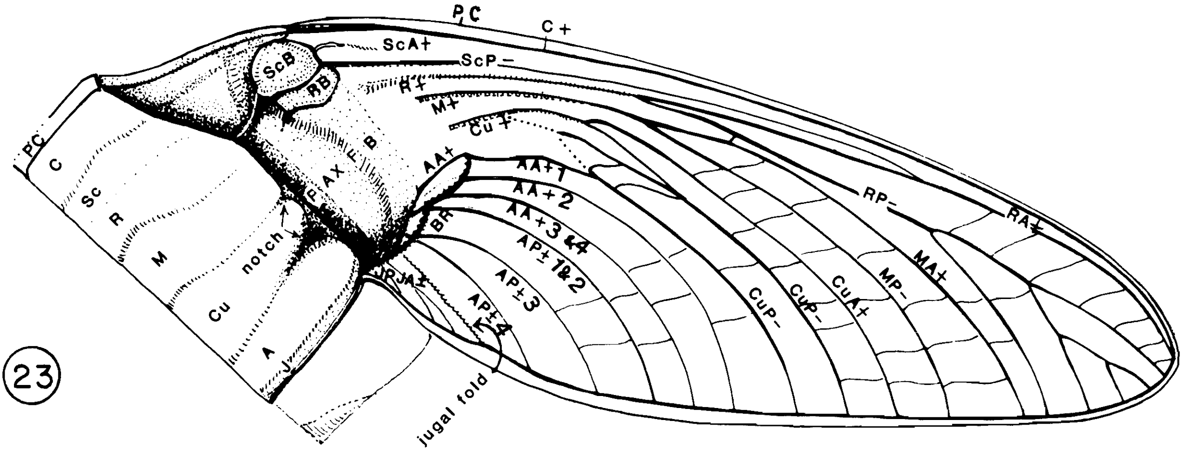
The main contribution of paleodictyopterid nymphs to evolutionary morphology is that even very young, primitive forms had a well-developed articular band with more or less defined sclerites. Their wings were at the same time curved, short, and obviously little or not functional for flapping flight (Figs. 19–28). The presence of well-formed sclerites in young primitive nymphs is probably due to the mobile ancestral condition which was in the process of being suppressed in juveniles.

The nymphs were terrestrial, probably mostly arboreal, and had a powerful, long, stiff beak. They likely fed on strobili, sucking in the contents of ovules, spores, and pollen (Kukalová-Peck 1983). A metamorphic instar was not necessary because wing articulation was still present and the growth of wings was gradual (Kukalová-Peck 1978). Many nymps had an exceptionally heavily sclerotized dorsum and looked like trilobites (Kukalová-Peck and Richardson, Fig. 12). In Recent insects, a "trilobite" shape occurs in forms that adhere closely to surfaces or live under surfaces such as bark. The large, heavily sclerotized nymphs were either nonflying or capable only of controlled gliding and probably stayed with or near the strobili.

In spite of their modified and partly or entirely immobilized wings, all paleodictyopterid nymphs that I know of (almost all available specimens) had a well-defined articular region. This includes *Rochdalia parkeri* and *Idoptilus onisciformis* studied by Wootton (1972, 1981*a*) which lost most, but not all, of their articulation to "scalping" when the rock was split open. This or any other secondary damage is meaningless to evolutionary considerations and must not be included in reconstructions (see Wootton 1981*a*, for an opposite suggestion).

The young homoiopterid nymph *Adolarryia bairdi* (Kukalová-Peck and Richardson, Figs. 13A, 13B) (Figs. 19–22) shows an incomplete articular band, because several posteromesial sclerites were scalped from the imprint and lost when the rock split open. Two additional nymphs with well-preserved articulation are introduced for comparison: *Paimbia fenestrata* Sinichenkova, 1979 of the specialized family Tchirkovaeidae, and *Parathesoneura carpenteri* Sharov and Sinichenkova, 1977 of the primitive family Homoiopteridae. *Paimbia* (Figs. 23, 25, 26) is probably the paleodictyopterid nymph with the best preserved articulation. This is very similar to that of the homoiopterid *Adolarryia* (Figs. 19–22). In both specimens, the articular band meets the tergum at a deep, undulating groove and is elevated high above the tergum, while it gradually slopes distally towards the wing. The shape and convexity of the articular region in both nymphs is very close to that of adults (Figs. 16A, 16D). However, the more specialized *Paimbia* had a novelty: a retarded development of most (but preferential development of some) sclerites (Fig. 23). Apparently, a nymph with such impaired articulation had almost immobile wings.

The wing of the primitive nymphal homoiopterid *Parathesoneura carpenteri* Sharov and Sinichenkova, 1977 is curved, tapers abruptly, and has a small anal lobe, all features typical of a young nymph. In spite of this, it also has a fully formed axillary plate composed of fused subcostal through jugal basivenalia and fulcalaria (Figs. 24, 27, 28). Sutures between sclerites are clearly visible except between the medial and cubital basivenale and fulcalare, which fused together almost without a trace. The wing of this young nymph separated from the body with the axillary plate attached to it, a separation also typical of adults. Except for the stem of the radius, all veinal bases hinged to the axillary plate have alternating bands of thicker and thinner cuticle. This arrangement corresponds to a typical adult adaptation for gliding in which the radius is firmly fused with the axillary plate and the rest of the veins are flexibly hinged to it. Since the nymphal wings were short and curved, perhaps there was a need for very flexible hinges which were provided by alternations in thickness of veinal cuticle (Wootton 1981*b*). There is strong circumstantial



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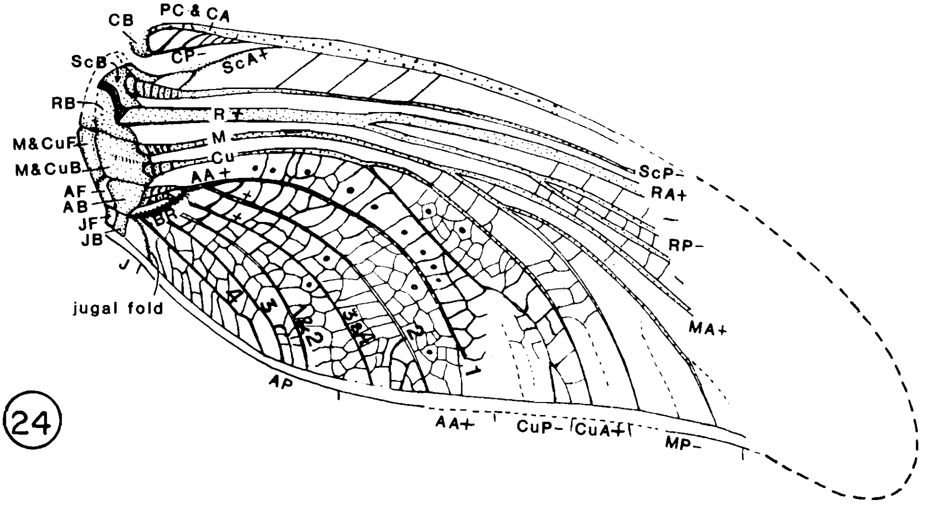

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FIG. 23. Paleodictyoptera, Tchirkovaeidae, middle-aged and specialized nymph. The articular region shows only two fully formed sclerites (ScB and RB). The central basivenalia and three veinal bases are scalped. The wing might have been partly fused with the tergum and was in all probability immobile. Note the almost regular tergal sulci and well-developed jugal area. *Paimbia fenestrata* Sinichenkova, 1979, paratype No. 2293/7; wing length 16 mm; Upper Carboniferous (Stephanian), Tungusk Basin, Siberia. Original drawing from the paratype. FIG. 24. Paleodictyoptera, Homoiopteridae, young primitive nymph with abruptly tapering wings that are fully articulated as in adults. Articular sclerites in the axillary plate are individually delimited by sutures, except for M and Cu basivenalia and fulcalaria, which became secondarily fused. The basal sections of wing veins other than R were flexible because they are formed by alternating strips of thicker and thinner cuticle, perhaps for flying in short hops on limited airfoils as in modern brachypterous insects. Note CP− starting from C basivenale (CB), and ScA+ starting from Sc basivenale (ScB). The nymphal wing was separated from the tergum with an adjacent axillary plate as is typical in the adults and was very likely mobile. *Parathesoneura carpenteri* Sharov & Sinichenkova, 1977, paratype No. 3115/26; wing width 11.5 mm; Upper Carboniferous (Stephanian), Tungusk Basin, Siberia. Original drawing from the paratype.

evidence that a *Parathesoneura* nymph, in spite of the awkward shape of the wings, was capable of limited gliding flight, as recognized previously by Sharov and Sinichenkova (1977).

As discussed earlier, primitive paleodictyopterid nymphs, even when they were young, had an articular band with clearly expressed sclerites and very likely were capable of limited flying. This probably is not true in more specialized Paleodictyoptera. In more advanced forms, delimitation of sclerites within the sclerotized articular area was retarded and sclerites were formed selectively. The first sclerites to occur were the subcostal and radial basalare, perhaps because of an involvement in gliding, and the precostal row of sclerites, perhaps because of its role in pronation of the wing.

The "narrowed wing base" as used by Wootton (1981*a*) for nymphs of Paleozoic Paleodictyoptera is an inexact term. In younger instars, the wing base always stretched along the full length of the scutum and scutellum; in older instars, the anojugal area often became widened, so that the wing base looks "narrowed" but in reality may be equally wide.

I previously believed that the heart-shaped prothoracic wings of adult and nymphal Paleodictyoptera were narrowly attached, only in the middle (Kukalová-Peck 1978). This interpretation was wrong because the homoiopterid juvenile described by Kukalová-Peck and Richardson 1983 (Fig. 13A) shows a rather well-preserved, vestigial, striplike articular region, bordering the entire proximal margin of the prothoracic wing (also in Neoptera, Fig. 17C). This makes more sense because it shows the prothoracic wings to be as broadly attached as pterothoracic wing pads. This reinforces the idea that all three pairs of thoracic wings started as fully, serially homologous.

The size ratio between wing and tergum is different for Paleozoic and modern nymphs (see Kukalová-Peck 1978, Figs. 29 and 30), and cannot be used to estimate nymphal age as proposed by Rasnitsyn (1981, p. 334). Recent nymphs have relatively much shorter wings because adult length is gained by a "leap" in the metamorphic instar. In young Paleozoic nymphs, the tergum to wing ratio is similar to that of much older modern nymphs, because the increase in wing length was formerly completely gradual. Diminished wing size of Recent nymphs contributed to survival of juveniles and occurred in all evolutionary lineages. Younger nymphs of Paleodictyoptera were distinguished by more posteriorly curved wings, a posterior wing margin confluent with the postscutellum, a thicker wing membrane, broader veins, fewer distinguishable veinal branches, and less distinctly delimited sclerites in the articular band.

Immobilization of nymphal wings and metamorphosis

The preceding discussion shows that primitive homoiopterid nymphs of Paleodictyoptera had a well-formed, functional articulation early in their ontogeny. In all probability they were able to fly, perhaps for short distances like a brachypterous insect may do today (J. A. Downes, personal observation). In contrast, the specialized tchirkovaeid nymph had a similar, well-sclerotized articular area, but the sclerites were weakly outlined and mostly unrecognizeable, so that the wing must have been immobilized. Apparently, the adaptive trend towards nymphs with nonmovable wings, which is common to all pterygotes, first expressed itself in Paleodictyoptera, in the more specialized families and then early in the ontogenetic series.

A comparable ontogenetic trend was observed by Rasnitsyn (1981) in some Russian Paleozoic Neoptera. He described several neopteran nymphs that apparently had nonmobile wing pads in younger instars, but movable and articulated ones in older instars. This discovery seems important because it was known previously that many Neoptera had already developed immobilized wing pads in the Paleozoic (Kukalová-Peck 1978) but by an unknown mechanism.

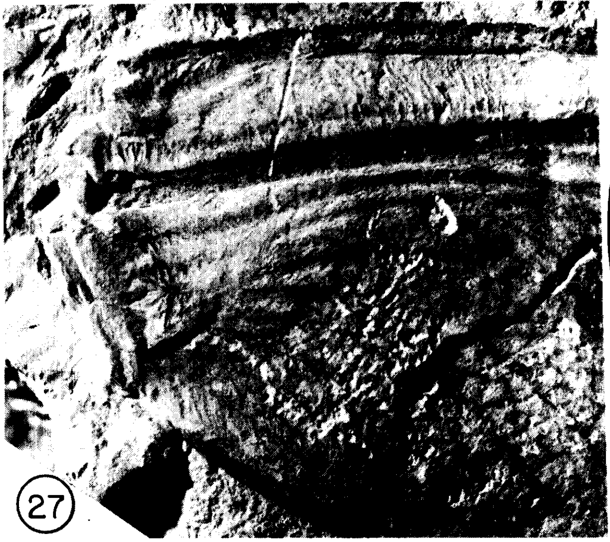
In my opinion, there is a common denominator to these two observations: the immobilization of nymphal wing pads probably started in young nymphs as a delayed break-up of the articular region into sclerites and proceeded into older instars, until the metamorphic instar was necessary. It also resulted in some wing pads looking like laterally extended, doubled tergal lobes (paraterga of other arthropods).

Rasnitsyn (1981) offered a different explanation: movable pro-wings, possibly subcoxal exites, were immobilized and fused with the tergum to form part of the complex paranota. They were separated again to become wings, by the mechanics described by the paranotal theory (see "Pleural origin of wings" for critical comments). In the external structure of all known Paleozoic Paleoptera, there is no sign of any part of the articular band being derived from the tergum.

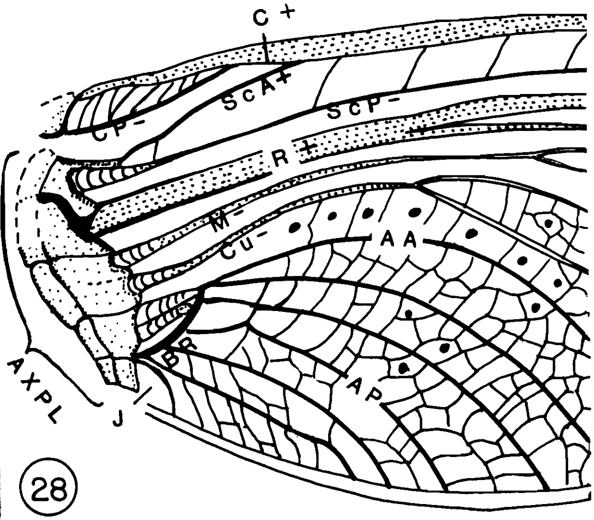
FIGS. 25 and 26. Paleodictyoptera, middle-aged and specialized tchirkovaeid nymph with well-defined articular area but incompletely developed articulation; wings were probably secondarily immobilized. Development of sclerites is retarded; only two basivenalia (ScB, RB) are fully delimited. Note the regular sulci on the tergum. *Paimbia fenestrata* Sinichenkova, 1979, paratype No. 2293/7; wing length 16 mm; Upper Carboniferous (Stephanian), Tungusk Basin, Siberia. Obverse and reverse printed and illuminated to look alike. Photo by Dr. Sinichenkova, Paleontological Institute, Academy of Sciences U.S.S.R., Moscow. FIGS. 27 and 28. Specimen and interpretation of a young, primitive, homoiopterid nymph with well-developed articulation; sclerites are fused into a typical adultlike axillary plate (AXP) and wings were very probably functional but with limitations. Note that only the radius (R) is fused with the axillary plate, while other veins are hinged. *Parathesoneura carpenteri* Sharov & Sinichenkova, 1977, paratype No. 3115/26; wing width 11.5 mm; Upper Carboniferous (Stephanian), Tungusk Basin, Siberia.

(25)

(26)



(27)



(28)

(Rich additional documentary material will be published in a later paper.)

The curved shape of the wing pads is a secondary adaptation for forward movement (Kukalová-Peck 1978). With each ecdysis, the nymphal bend of the wing straightened until it totally disappeared in adults. The metamorphic instar was missing. A residual bend in a homoiopterid subadult wing is shown by Kukalová-Peck and Richardson (1983) in Fig. 14 (arrow).

It should be mentioned perhaps that a metamorphic instar is a specialization which evolved only in some arthropods. In fact, repeated moulting cycles in adulthood are commonplace, and only specialized crustaceans and specialized arachnids gave up adult moulting. The sister group of pterygotes, the Thysanura, moult continuously and do not have a metamorphic instar. Pterygotes dropped multiple subadult and perhaps also adult moulting during the recorded fossil history, and there is strong fossil evidence that this process happened in parallel in several lineages (Kukalová-Peck 1978). It would likely be a misconception to presume that the metamorphic instar of higher categories must be comparable for "age" and for the number of incorporated previous instars. The ontogenetic series could have stopped at approximately the middle or anywhere else before maturation, so that the metamorphic instars may not only be unequally "old," but also represent a different number of fused original instars.

If the metamorphic instar was indeed an adaptive compensation for the delayed break-up of the articular region into sclerites, as documented by the fossil record, the event probably did not happen too late in nymphal development but somewhere near the middle. The metamorphic instar was probably originally followed by an unknown number of nymphal instars, subimagoes, and imagoes, all with fully articulated wings. A subimago is present in modern Ephemeroptera, but several subimagoes are recorded in Paleozoic Ephemeroptera, Paleodictyoptera, Megasecoptera (Kukalová-Peck 1978) and in primitive Neoptera (Sharov 1957*a*; this paper). Though in modern pterygotes subimaginal instars are mostly no longer apparent they were present in past developmental series and, therefore, they must have been absorbed in the modern series by other instars. Perhaps they are expressed in modern insects by delayed maturity after emergence from the metamorphic instar. This delayed maturity occurs elsewhere in Pterygota, i.e., in the teneral adults of Odonata (E. L. Smith, personal communication) and in the cricket *Acheta domestica* (Bocharova-Messner 1968). A detailed comparative study is needed to provide documentation.

In the Recent fauna there are examples where the imago becomes absorbed by the subimago, namely in females of the mayfly *Dolania americana*, which mates and oviposits as a subimago (Sweeney and Vannote 1982). Clearly, the metamorphic instar is one of the most plastic structures of pterygotes, perhaps partly because of its comparatively late appearance on the evolutionary scene.

There is no doubt that the number of instars in Paleozoic insects was much larger than in modern insects (Kukalová-Peck, 1978). Hence, absorption of instars must have taken place in much of the ontogenetic series. However, as far as the condition of wings and articulation are concerned, modern juveniles remind one of younger instars while older nymphs and subimagoes, with one exception (mayflies), are missing. This fact seems to support the hypothesis that the metamorphic instar evolved (possibly in all pterygotes!) not between juveniles and adults, as previously supposed, but within the juvenile series itself. The older juveniles were perhaps absorbed mainly into the adult stage.

The pitfalls of reconstructing the wing articulation

Paleontological reconstructions are a Damoclean sword. They give a clear, uncluttered image of the organism and therefore are necessary and important as a progress report. On the other hand, they reflect bluntly whatever shortcomings there are in the current evidence or interpretation and are open to criticism, both by the well-informed and the not-so-well-informed scientific community. The accepted compromise is to figure clearly only well-known features, and to leave out or only vaguely indicate imperfectly known features. A reconstruction, of course, must never include preservational artifacts, and it is expected that it should be improved as new material is discovered. Rejected reconstructions, quite understandably, abound in the literature and are recycled in current textbooks and elsewhere years after they have been recognized as faulty and replaced. Entomologists are often unaware of their special, "perishable" nature and treat them with the same confidence as figures of living specimens which stay valid for centuries.

In a recent review, Wootton (1981*a*) criticized my reconstructions of two paleodictyopterid nymphs *Idoptilus onisciformis* and *Rochdalia parkeri* (Wootton 1972; Kukalová-Peck 1978, Figs. 22, 24) for "inexactly" figuring the articular region and trailing edge. Unfortunately, in both specimens the articulation was almost completely scalped (see "Working with fossils"), and the few sclerital remnants did not provide enough information for a good reconstruction. The two nymphs were shown for the spectacular curvature of their wing pads, and the lack of knowledge about articulation was indicated by the vacant strip parallel to the terga. I was able to improve and complete my reconstructions only recently; the missing evidence on nymphal articulation, etc., is presented in a companion paper in this issue (Kukalová-Peck and Richardson 1983, Figs. 12, 13A).

Including preservation state in the reconstruction as Wootton suggests, to make it more "truthful," would lead to a never-ending confusion about which features are actually preserved and which are proposed as genuine morphology. A reconstruction must give the "alive" image by all means possible.

In some pterygote nymphs, the postscutellum and posterior "trailing" edge of the wing pad are confluent. Confluency occurs only if the anojugal area of the wing is small, as in young nymphs, and is especially frequent in young cockroaches. Stonefly nymphs sometimes have the confluent edge in fore wings but not in hind wings, which are basally broader. In paleodictyopterans, the confluent edge is a good diagnostic character for young nymphs because the anojugal area becomes expanded rather early in ontogeny (Figs. 19 and 20 compared with Figs. 25 and 26).

Morphologically, the confluent edge is the tergal overhang (= postscutellum) fused with the articular overhang posterior to the jugal row of sclerites, and this is fused with the confluent posterior wing margin. The combined overhang-overhang-wing margin serves in adults as an important blood duct, the axillary cord. This asymmetrical structure was very likely acquired during development of flapping flight and does not give support to the paranotal theory!

Major divisions of Pterygota

As reviewed recently by Kristensen (1981), the monophyly of Pterygota is widely accepted, except by Lemche (1940), Smart (discussion in Wigglesworth 1963), Matsuda (1970, 1981), and LaGreca (1980). Monophyly of Neoptera is probably universally acknowledged, but Paleoptera are considered by some entomologists as a grade, not as a monophyletic taxon (Boudreaux 1979; Rohdendorf and Rasnitsyn 1980; Rasnitsyn 1980; Kristensen 1981; Matsuda 1981). However, the fossil evidence shows that these authors concentrated on an erroneous set of characters, of a mostly autopomorphic–convergent, or else plesiomorphic, nature. Since the pterygotes emerged as a group with the occurrence of wings, it is this structure that is of prime phylogenetic importance at the dawn of their evolution. The first split of Pterygota concerned wings and articulation, while other characters such as mouthparts are certainly very significant before as well as after the split, but cannot be mixed with the event itself! This fact would seem obvious to the cladists, but it has not been recognized for its importance. Paleoptera and Neoptera have a long history of character misconceptions.

Hennig (1981, p. 132) believed that Paleoptera and Neoptera are sister groups and that their origin is the earliest recognizeable event in the phylogenetic history of Pterygota. At the same time, he complained that the characters shared between Recent Ephemeroptera and Odonata seem meager, such as a short bristlelike antennal flagellum, the intercalar veins in the wings, and fused lacinio-galea in the maxilla. Martynov (1924) defined Paleoptera by the lateral or vertical position of wings at rest and by the absence of a jugal area (neala).

The presently known fossil record shows most of the above-mentioned characters not to be panpaleopteran. Antennae in Paleozoic Ephemeroptera and Protodonata were not bristle like, but moderately sized. Intercalar veins were missing in most Paleodictyopteroidea. A lateral or vertical position of the wings did not occur in Diaphanopterodea because they folded their wings backwards. A jugal area (neala) is present in Paleodictyoptera, Paleozoic Protodonata, Paleozoic Ephemeroptera and, in a reduced state, in Recent Ephemeroptera and Odonata.

Shared basic characters of Paleoptera observable in the fossilized state and in modern forms are different: a similar basic veinal pattern and fusions, a bandlike arrangement of dorsal articular sclerites, the presence of composite axillary plates in gliding forms, an absence of composite axillary sclerites, an absence of turning–pivoting type of composite sclerites (3Ax), the presence of sclerites at the cubital level in both gliding and nongliding forms, a paleopterous type of venational fluting, tergal lobes serving as "articular processes", a fused laciniogalea, and an absence of trochantin.

The oldest odonatoids have venation very similar to that of Paleozoic Ephemeroptera (Fig. 3; Riek 1970, p. 173; E. F. Riek, in preparation).

The first divergence within Pterygota very likely was triggered by adaptation to flight and to different feeding strategies, and the initial structural transformations most probably affected evolution of the wing articulation, wing venation, and mouthparts, as follows.

From what we now know, the ancestral pterygote had primitively, probably incompletely, foldable wings hinged by a band of sclerites, and each mandible with only one permanent condyle posteriorly (the original leg articulation on the mandibular head segment[14]), while the anterior mandibular condyle was temporary and activated by voluntary pressure of the mandible against the labral segment. This type of mandibular articulation still exists in thysanurans and in juvenile ephemeropterans (E. L. Smith, personal communication) and has been found in all suitable preserved Paleodictyopteroidea examined (Kukalová-Peck 1983).

Ancestral pterygotes gave rise to at least three major paleopterous lineages: Paleodictyopteroidea, Ephemeropteroidea, and Odonatoidea (the last two are probably

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[14] More precisely, articulation of mandibular subcoxa on the mandibular epicoxa incorporated in the head capsule under the eye.

sister groups). Members of each lineage adopted a different type of feeding and of flying, and gradually accumulated a large number of characters, which made them quite different. All groups except the paleodictyopteroid Diaphanopterodea eventually acquired gliding ability through linear fusions between at least one axial wing vein (R) and several sclerites of the articular band and used it for different major purposes: searching for scattered strobili (Paleodictyopteroidea), dispersal flight (Ephemeroptera), and hunting (Odonata). Plesiomorphic pterygote mouthparts remained virtually unchanged in Ephemeroptera and little changed but elongate in Paleodictyopteroidea, while predatory Odonata evolved a permanent anterior condyle, a necessary prerequisite for chewing up prey.

Did the immediate ancestor of Paleoptera have a fused laciniogalea in the maxilla? If there was a fusion, then Paleoptera must be separated as a group from the (hypothetical) "Protopaleoptera." Neoptera have unfused laciniogaleae which must have been retained from an unfused condition, either from the "Protopaleoptera," or from the early Paleoptera.

Neoptera diverged by aquiring a pivoting 3Ax, a device enabling these insects to fold and lock their wings back at rest, to hide more effectively, and to seek more varied food. They also gained, probably at about the same time and independently from Odonata, a permanent anterior condyle in the mandible, resulting in improved chewing ability. The combination of these two new characters opened for Neoptera a new, bright, and versatile evolutionary future and resulted in their becoming superior competitors of all plant-feeding Paleoptera (Paleodictyopteroidea) including the wing-folding Diaphanopterodea with their short, sucking, primitive beaks (Fig. 1).

Hennig (1981) introduced alternative evolutionary terms principally for use in the theoretical systematics of higher taxa: the stem group and daughter group. In paleontology (i.e., when considering the systematic position of higher categories) the sister group concept does not reflect phylogenetic asymmetry, which is frequent. For example, an ancestral stock could successively generate a number of lineages that became extinct and one successful one whose members radiated and reached the Recent epoch by many subbranches. It is probably not an exaggeration to say that most sister groups of living insect families and higher taxa are now extinct. Sometimes a several times removed cousin made it into the present. I consider Hennig's modified alternative model most useful and suggest that Paleoptera are a classical example of a stem group which yielded several successive side lineages diverging more and more from each other as time went by through accumulation of divided character changes (autapomorphy), but nevertheless maintaining (even though well masked) a closeness to the ancestral pattern. Neopterans seem to present an equally good example of a daughter group that was derived very early by acquiring few but fundamentally significant apomorphies. Some plesiomorphic characters were preserved in Neoptera but became obsolete in more specialized, surviving members of the stem group Paleoptera.

Evolutionary morphology has yet to provide a decisive answer as to how to classify the ancestral Pterygota. The fused lacinio-galea of all Paleoptera might well be an apomorphic character separating them from the ancestral "Protopaleoptera." In any case, paleopterous superorders are branches that diverged from an unknown ancestral line morphologically closest to Diaphanopterodea. There is, therefore, no reason to eliminate the category Paleoptera. Neoptera show a completely different trend in specialization of ancestral articulation and could have evolved from none but the oldest, unspecialized paleopterous pterygote. There is no closer relationship between any of the known paleopterous groups and Neoptera. All relations are via the common yet unknown ancestral form.

Arthropodan characters and evolution

To orient oneself in the maze of available arthropodan characters, many of which are insufficiently known for clear interpretation, one's theoretical attitude and background are very important.

Most evolutionists, most paleontologists, and many entomologists believe that all invertebrate structures, in their primary complexity including the panarthropodan body plan, came into being much before the beginning of the fossil record, which starts roughly at the base of the Cambrian. It should be emphasized that only one major animal group originated during the geological time recorded by fossils: the vertebrates. Arthropodan evolution documented in fossils shows mostly transformation of preexisting primary structures. These transformations are reductions in symmetry, number, relative size, or seriality, and occurred by fusion, simplification, disproportionate growth, membranization, shifting, etc. The most common theme of evolution seems to be the reduction and simplification of a primary structure and the transformation of its vestige, as expressed, for example, in the newly acquired metamorphic structures. "Added," secondary structures such as aphid cornicles, secondary genitalia of male dragonflies, etc., are structurally much more simple than the primary structures.

The "everything is possible" attitude certainly is not supported by the fossil record, just the opposite. The reduction-oriented evolutionary process affects egg, juvenile, and adult separately and extensively. Limbs, endites, and exites can be present in the embryo, absent in young nymphs, and then reoccur in the nymphs or adults. Wing articulation can be lost in the nymph, reappear in the metamorphic instar, and become functional in the subadult or adult.

A parallel or analogous macroevolutionary trend is also evident in vertebrates, most markedly in limb and skull evolution, in which reduction in number and seriality of bones is well documented. The basic, five-rayed tetrapod limb evolved from the multirayed walking fin of lobe-finned fishes and the skull bones, jaw, and inner ear from a segmented condition of multiple bones and gill arches. A basic, more serial, and multiple pattern in evolution of the vertebrate skull can be demonstrated for all osteichthyans and their derivatives, the tetrapods (Jollie 1981).

With this line of thinking, derivation of the asymmetrical, composite, and divergent articular sclerites of Recent Pterygota from the multiple, densely arranged, serial, unfused, and more symmetrical ancestral sclerites is not only possible but likely. The existence of the Paleozoic band of sclerites can likewise not be explained by any combination of articular features of modern insects, and cannot have originated as a "chance" structure.

To explain any structure within the pleuron or genitalia, the full, ancestral, panarthropodan leg model including endites and exites on the upper leg should be considered the primary source of possible homologues (Figs. 29A, 29B, 30A, 30B). Some parts of the insectan mouth and genitalia are based on endites, while exites of Paleozoic Pterygota probably gave rise to a series of wings. They provide direct evidence that the ground plan of the panarthropodan leg has survived since the Proterozoic. We now know that the leg was the primary organ supplying features distributed between the tergum and sternum, including abdominal styli, gonostyli, pleuropodia, ovipositor, claspers, gonapophyses, parameres, penes, and larval prolegs, and also fortification of the pleural body wall in the thorax and abdomen, the cerci, the wings, wing articulation, and abdominal paranota. Detailed homologization of leg structure of all arthropodan groups will be published in E. L. Smith's upcoming book.

I am not arguing against the existence of dormant genes, recurring structures, and conspicuous secondary "additions" such as subsegmentation of tarsus, annulation and elgonation of ceri, and development of intercalar veins, but I am reporting the macroevolutionary pattern and how it reveals itself in the fossil record. All existing "simple to complex" evolutionary models of the euarthropod leg or primary wing venation deal with either hypothetical processes which happened in the Proterozoic or are speculations never documented in the fossil record. Every "new" structure (i.e., nonhomologous within Pterygota) is a prime suspect for misinterpretation. A good example are the serial tracheal gills on the abdomen of mayfly nymphs which are equipped with appendicular muscles. Some suggested interpretations are that tracheal gills were derived from the tergum, from the subalare, or from a secondary gill. However, in arthropods the terga do not develop segmental appendages, the subalare does not evaginate, and there are no simple gills moved by muscles. With the reverse "complex to simple" model of evolution, which is documented massively by the fossil record, the musculated tracheal gill is a serial appendage traceable back to the more complicated panarthropodan leg and can be either an exite, a wing, or a leg, depending on its position.

Wing venation of all pterygotes is homologous to the last primary branch if the symmetrical ancestral model is used for comparison (Figs. 13–15). This model allows for the homologous interpretation of the "costal brace" of Ephemeroptera as ScA+, the "anal brace" of Ephemeroptera as a combination of several anal stems and branches, the "ambient vein" of Orthoptera as costa, the "precostal area" of Orthoptera as the C-ScA area of Pterygota, the "epipleuron" of Coleoptera as a precostal pair, the "postcubitus" of some Neoptera either as AA_2 or as $AA_{3\&4}$ of all Pterygota, the "plical vein" as CuP, the "empusal vein" as AA_2 or $AA_{3\&4}$, the "anal crossing" in Odonata as a section of CuP, etc. The fact that all primary veinal features thought at one time to be unique or only partly homologous are fully homologous throughout Pterygota confirms that the wings as well as the pterygotes are monophyletic.

My new "epicoxa and exite" hypothesis of wing origin is introduced here after many years of hesitating between several potentially eligible arthropodan structures. This hypothesis has to be tested against the question: Where is the epicoxa in the other arthropods?

Recent arthropods are so changed that existence of an epicoxal podomere perhaps cannot be convincingly documented. However, segmental features of the laterotergite in *Anaspides* were found by Carpentier and Barlet (1959). It is possible that the laterotergite is the euarthropodan epicoxa.

Obviously, the presence or absence of an epicoxa in the ground plan of the arthropodan leg can be solved most convincingly by presenting direct evidence in fossils. The legs of the oldest known Paleozoic (Cambrian) arthropods are currently being studied in detail by H. B. Whittington, D. F. G. Briggs, and J. L. Cisne. I approached all three paleontologists, but none was yet ready to make a comparison of the arthropodan upper leg. Therefore, the epicoxa and its exite is offered here as a morphological extrapolation based solely upon the

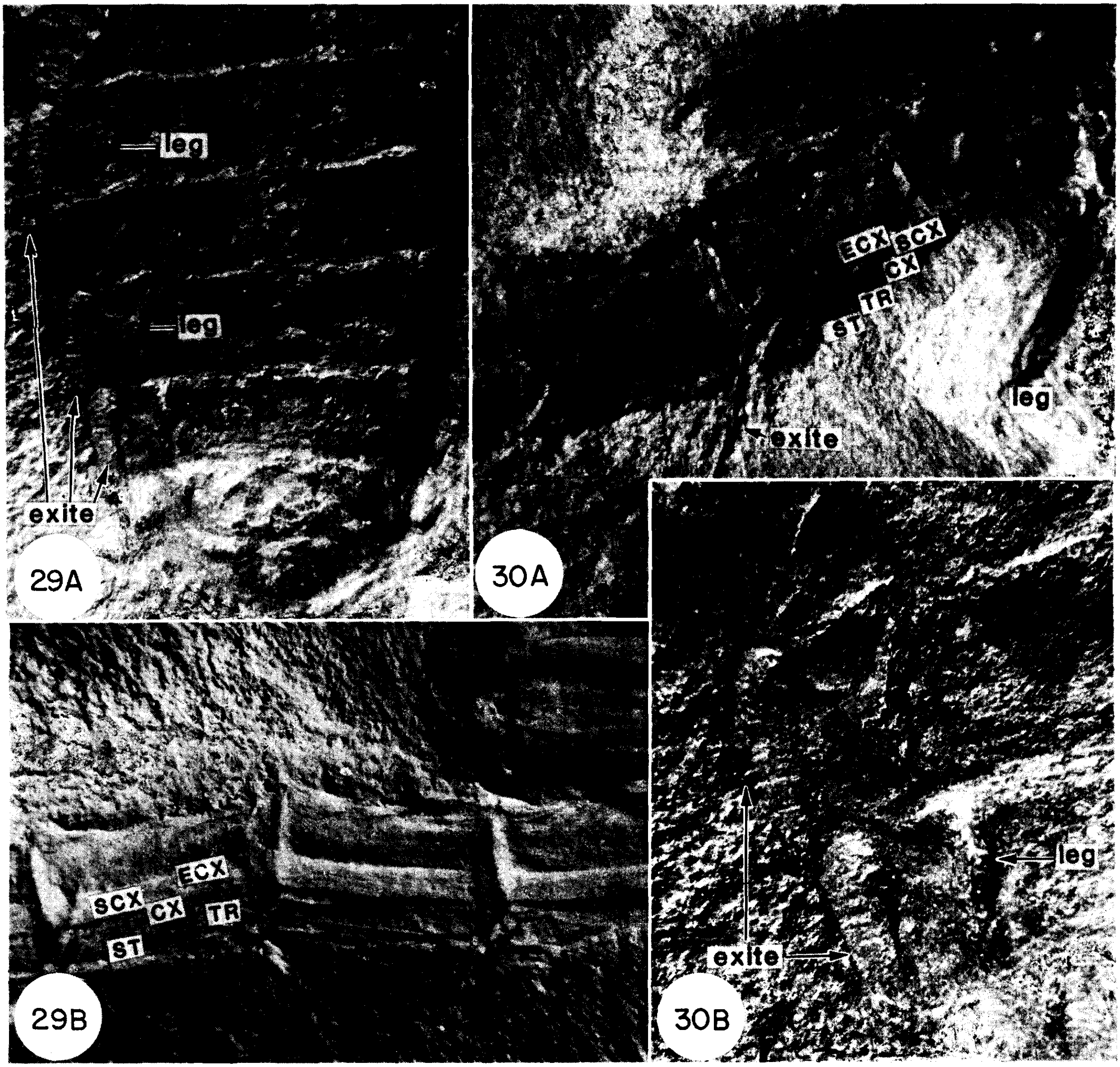

FIG. 29. (A and B) Neopterous insect probably related to *Eucaenus* (Carpenter & Richardson, 1976; Protorthoptera) with a full series of pregenital abdominal legs as well as annulated abdominal exites, homologous to the tracheal gills of Ephemeroptera, Odonata, Plecoptera, Megaloptera, sisyrid Neuroptera, and ?gyrinid Coleoptera. Specimen preserved ventral side up. Cuticle and appendages are partly scalped. Undescribed specimen No. 30370, Field Museum of Natural History, Chicago. Maximum width of abdomen, 10.8 mm; maximum length of exite, 2.9 mm; Upper Carboniferous (Westphalian C–D), Illinois.

FIG. 30. (A and B) Protodonate nymph, uncoated (A) and coated with ammonium chloride (B), showing the abdominal pleuron primitively divided by sutures into plates, including the keeled epicoxa (ECX), sloped subcoxa (SCX), narrow coxa (CX), slightly broader trochanter (TR), and sternum (ST). Tracheal filaments, identified here as epicoxal exites, are articulated under the epicoxa (middle exite in A). Undescribed specimen No. PE 30272, Field Museum of Natural History, Chicago. Maximum width of abdomen, 4 mm; Upper Carboniferous (Westphalian C–D), Illinois.

study of fossil insects. Hopefully, supporting evidence in early Paleozoic marine arthropods will eventually emerge.

Epilogue

Integration of modern and fossil morphological data, as proposed in this account, might seem to lead to an unorthodox interpretation of insect evolution. However, just the opposite is true as far as major evolutionary principles are concerned.

The evolution of insect wings, in the paranotal theory, is contradictory to two natural "rules": (*i*) glider specialists never flap their gliding planes while gliding and therefore (for many reasons, Kukalová-Peck 1978) cannot develop flapping wings, and (*ii*) flapping wings in all other animals are derived from a limb or part of a limb. The alternative explanation, based here on fossils, that insect wings are leg appendages which were primitively articulated, allows insects to have followed an evolutionary path comparable to that in other animals. From the same point of view, the paranotal theory is highly unorthodox as well as unlikely; according to this theory, insects would appear to have been controlled by evolutionary mechanisms different from those which guided the evolution of other flying animals.

The earliest division of Pterygota is usually believed to be into Paleoptera and Neoptera (Hennig 1981). The characters supporting this division, however, were so inconclusive that alternative phylogenies have been proposed at an increasing rate. The fossil record though, in contrast to modern morphology, shows the basic derivative characters which confirm the soundness of this division.

A monophyletic origin of wings seems to be quite obvious. However, previous evolutionary venational schemes were inadequate and did not cover all veinal characters of all orders. Ephemeroptera, Odonata, Orthoptera, and Coleoptera appeared to have "additional" and nonhomologous veinal features. The fossil record offers a remedy by giving clues to a richer and more symmetrical ground-plan venational system from which the venation of all orders can be derived without the use of nonhomologous vein names.

A monophyletic origin of wing articulation also seems quite obvious, yet the previously accepted ground scheme of articular sclerites, based upon Neoptera, leaves some articular sclerites of modern Paleoptera unexplained. The fossil record indicates that the ancestral pterygote articulation was not of a neopterous type but much richer and gave rise to a different paleopterous and a different neopterous articulation. Thus, the fossil evidence does not upset a general belief, but explains it in an evolutionarily more likely way.

Metamorphosis (defined as the presence of a metamorphic instar) is a relatively late specialization, which occurred partly during the time period documented by fossils, and only in the most advanced group of insects, the pterygotes. All modern pterygotes metamorphose; however, several orders of Paleoptera and some Neoptera in the late Paleozoic had continuous development. Consequently, metamorphosis must have originated after the split into Paleoptera and Neoptera and is of necessity polyphyletic. A division into the formal groups Hemimetabola and Holometabola is therefore invalid. This conclusion was recently indirectly supported by Hennig (1981) who pointed out a number of characters showing that holometabolous Endopterygota are probably a sister group only to the hemimetabolous Paraneoptera.

Hennig's suggestion seems to have recently found additional support in the fossil record. The primitive neopterous family Strephocladidae, which have conspicuous macrotrichia on their wings and were considered to be related to the Endopterygota by Carpenter (1966) and Kukalová-Peck (1978, p. 85), were recently recognized as paraneopterous (Order Hypoperlida: Rasnitsyn 1980; Rohdendorf and Rasnitsyn 1980). Their mouthparts have laciniae which are chisellike in shape, similar to those of some psocopteroids (personal observation in 1982, PIN, Moscow). Strephocladids possibly belong to the stem group of the Acercaria (sensu Hennig 1981).

It has long been agreed that Archeognatha (machilids) are the most primitive ectognathous insects: the "stylus" on their thoracic coxae has sometimes been compared with the leg exites of some myriapods and crustaceans, but other interpretations have also been offered, including the highly unlikely "newly developed" appendage (by Manton 1977). Now that annulated exites have been found on the upper leg segments of primitive fossil (and probably also modern) pterygotes, the archeognathan coxal stylus is proved to be a plesiomorphic, euarthropodan, residual structure: an exite. More importantly, exites in pterygotes are leg derived, articulated, euarthropodan appendages and are eligible by their position, preadaptive function, and muscle armament to be predecessors of wings.

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List of abbreviations

A = anal
AA = anal anterior (sector)
AB = anal basivenale
AF = anal fulcalare
AP = anal posterior (sector)
AT = antenna
AX = axalare
AXJ = jugal axalare
AXPL = axillary plate
B = basivenale
BA = basalare
BR = brace
BT = basitarsus
C = costa
CA = costa anterior (sector)
CB = costal basivenale
CP = costa posterior (sector)
cr = cross veins
Cu = cubitus
CuA = cubitus anterior (sector)
CuB = cubital basivenale
CuF = cubital fulcalare
CuP = cubitus posterior (sector)
CX = coxa
ECX = epicoxa
END = endite
EX = exite
F = fulcalare
gb = segmental gill, filament
FE = femur
J = jugal
JA = jugal anterior (sector)
JB = jugal basivenale
JF = jugal fulcalare
JP = jugal posterior (sector)
JB = jugal basivenale
L = tergal lateral lobe
LR = labrum
M = media
MA = media anterior (sector)
me = membrane
MD = mandible
MP = media posterior (sector)
MX = maxilla
P = proxalare
PA = anal proxalare
PAT = patella
PC = precosta
PCA = precosta anterior (sector)
PCP = precosta posterior (sector)
PCu = cubital proxalare
PFE = prefemur
PIN = Paleontological Institute of the Academy of Sciences in Moscow
PJ = jugal proxalare
PM = medial proxalare
PP = pleuropodium
PRO = pro-wing
PT = posttarsus
R = radius
RA = radius anterior (sector)
RB = radial basivenale
RP = radius posterior (sector)
S = spiracle
Sc = subcosta
ScA = subcosta anterior (sector)
ScB = subcostal basivenale
ScP = subcosta posterior (sector)
SCX = subcoxa (pleuron)
T = tarsus
TE = tergum
TI = tibia
TR = trochanter
VWP = ventral wing process
W = wing or winglet