

# The Evolutionary Pathway to Insect Flight – a Tentative Reconstruction

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*Received 15.xi.2007, accepted 25.iii.2008.*

*Published online at [www.arthropod-systematics.de](http://www.arthropod-systematics.de) on 30.vi.2008.*

## > Abstract

Studies on non-pterygotan Ectognatha revealed that the construction of the winged Pterygota is based on lepismatid organization and that the first steps of mastering the air were attained already in the common ancestor of Ectognatha by adaptations in the context of jumping which is still retained in Machilidae (Archaeognatha). In these, the terminalfilum and the ectognathan 3-segmented antenna permit attitude control of the body. The acquisition of the mandibular dicondyly led to climbing on vascular plants and exploitation of plant tips as food since the late Silurian. The problems of beginning sustained flight with flapping wings are discussed. A scenario with intermediate gliding and one without gliding are presented. The corresponding parts of the sclerites and muscles of the three subcoxal leg segments found in lepismatids are still recognizable in the pterygotan pterothorax. The wings are composed of the paranota and part of the most basal subcoxal leg segment. It is concluded that wing elongation was impossible without flexing the wings on the back already during early evolution and that the inability to flex the wings is secondary. Wing flexing nearly ab initio was possible by a mechanical switch between the states of flight and non-flight. This led to the neopterous construction of the wing base.

## > Key words

Ectognatha, Machilidae, Lepismatidae, jumping, dicondyly, pleural sclerites, wing articulation, attitude control, gliding, flight.

## 1. Introduction

When trying to reconstruct the evolution of insectan wings there are two main questions to be answered. One is the question which were the precursor structures of the wings. The other is how the scenarios were composed that caused the selection which transformed the precursor structures into wings capable of sustained flight. As regards the first question two conceptions are still in contention: the exite theory of J. Kukalová-Peck and the classical paranotal theory.

KUKALOVÁ-PECK (1978, 1983, 1985, 1987) assumes that the precursors of the wings were exites of the epicoxa, the more proximal of two subcoxal leg segments. She proposes that both segments became incorporated into the body wall and that the epicoxae were fused with the sides of the terga thus forming the tergal lobes (paratergites) in all body segments, even in apterygote Hexapoda and other Euarthropoda. In her view the protopterygotes had aquatic juvenile stages in continuation of an aquatic arthropod ancestor and the exites were movable gill plates on all body segments, similar

to the gill plates in nymphs of Ephemeroptera, which are regarded to be the serial homologues of wings (KLUGE 1989 after BRODSKY 1994). All primarily apterous Hexapoda became fully adapted to terrestrial life. For the next step – using the gills as airfoils by adults – KUKALOVÁ-PECK (1987) assumes that the nymphs of the pterygote ancestors left the water, moulted to the aerial stage and evolved the flight ability. The problem that the gill plates were large enough to create water currents but were not large enough to act as airfoils was tried to be solved by MARDEN & KRAMER (1994, 1995) and MARDEN (2003). Observed skimming on the water surface by wind in some Plecoptera was thought to be a suitable intermediate stage. RASNITSYN (2003) analyzed the possible scenarios of this conception and concluded “that skimming locomotion descended from flight rather than preceded it”.

The paranotal theory assumes that the precursors of the wings were immovable paranota, i.e., pterothoracic paratergites or lateral lobes of the tergites as

they are found in apterygote Hexapoda (especially in Lepismatoidea), regardless of whether they are lateral outgrowths of the terga or originally basal leg parts. It is assumed that the ancestors of Pterygota climbed on vascular land plants and utilized favourable descent by falling down and gliding. This led to the movability of the paranota and sustained flight with flapping wings. QUARTAU (1985, 1986) presented a very comprehensive and critical overview of the literature on the paranotal theory. His main objection against it is the insight that selection which favours gliding does not favour flight by flapping wings. It is one of the aims of the present work to discuss this problem in more detail in connection with suitable scenarios (sections 2.2.2., 2.2.3.). The reinterpretation of a pair of fossil mandibles revealed that the advanced mandible type of (Meta-)Pterygota (ball-socket construction of the anterior articulation) existed already in the Lower Devonian (ENGEL & GRIMALDI 2004) suggesting that flying insects evolved at a time when the land plants were apparently not high enough to permit effective gliding. This problem is likewise discussed in section 2.2.3.

The functional aspects of the beginning of flight were studied by falling and wind tunnel experiments using models. Addition of small horizontal plane appendages to cylindrical models did not significantly improve the aerodynamic abilities (FLOWER 1964; KINGSOLVER & KOEHL 1985). It was therefore looked for other reasons which might be responsible for enlarging the planes until they were of suitable size. The proposals were: the small planes were firstly engaged in (1) attitude control (FLOWER 1964; HINTON 1963), (2) thermoregulation (WHALLEY 1979; KINGSOLVER & KOEHL 1985, 1989), (3) dispersal by utilizing passive transport by air currents (WIGGLESWORTH 1963, 1967; NORBERG 1972 – critique by ELLINGTON 1991).

Contrary to these notions, I was able to show experimentally that both attitude control and gliding ability are already realized in Lepismatidae, the closest relatives of Pterygota (HASENFUSS 2002). They may have retained features of the common ancestor and present thus a situation similar to that the wing evolution started from. Living lepismatids fall always on their feet by utilizing the drag of the caudal filaments (cerci and terminal filament) and outstretched antennae. Furthermore, lepismatids are adapted for extremely fast running and hiding in flat crevices into which predators cannot follow. The dorsoventrally depressed body forms a comparatively large ventral plane with rearwardly appressed flat legs. Falling experiments with models of lepismatid size, shape, and weight revealed the – in principle – possible ability to glide. Attitude control and perhaps gliding ability appear thus as preadaptations that were acquired long before the wing evolution began. It was therefore desirable to study the

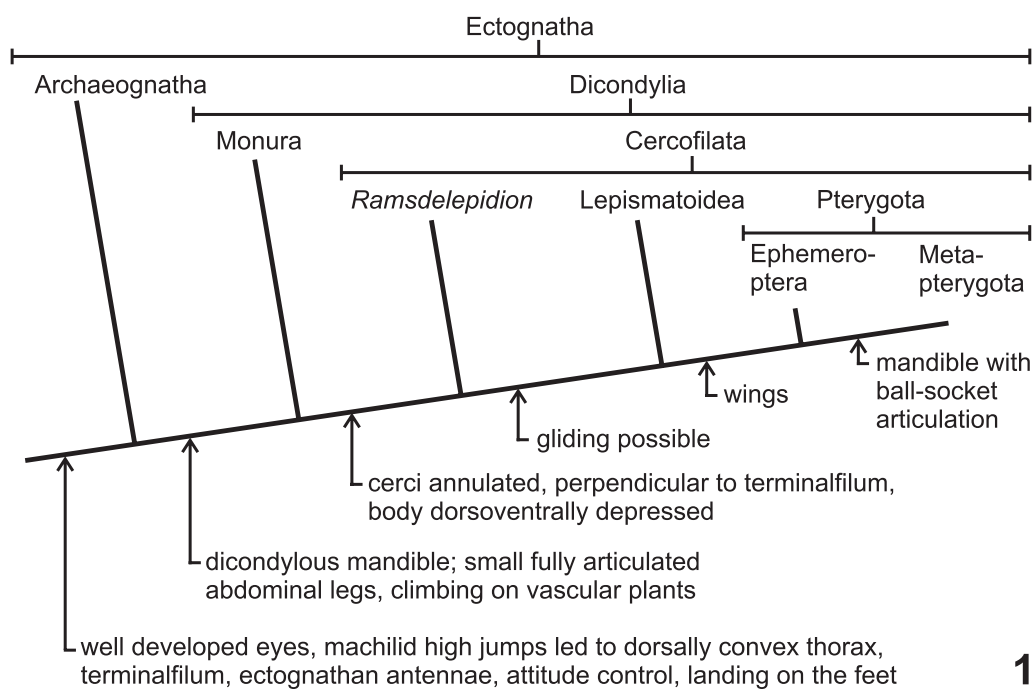
other primarily wingless Ectognatha more closely in order to find the conditions which led to the preadaptations on the way to insect flight (sections 2.1.–2.2.1.).

The functional anatomical study of the mesothoracic skeleto-muscular organization in *Lepisma* showed the possibility that the paranota could become movable simply by introducing dorsally a strip of weakness at their base and utilizing the articulation between the two basal of three subcoxal leg segments as the wing articulation (HASENFUSS 2002). Flapping movements were automatically possible by the already existing muscles. This is substantiated by the homology of many muscles in *Lepisma* and Pterygota; some of them are, in Pterygota, bimodal and are used alternatively for leg and wing movement (MATSUDA 1970; HASENFUSS 2002).

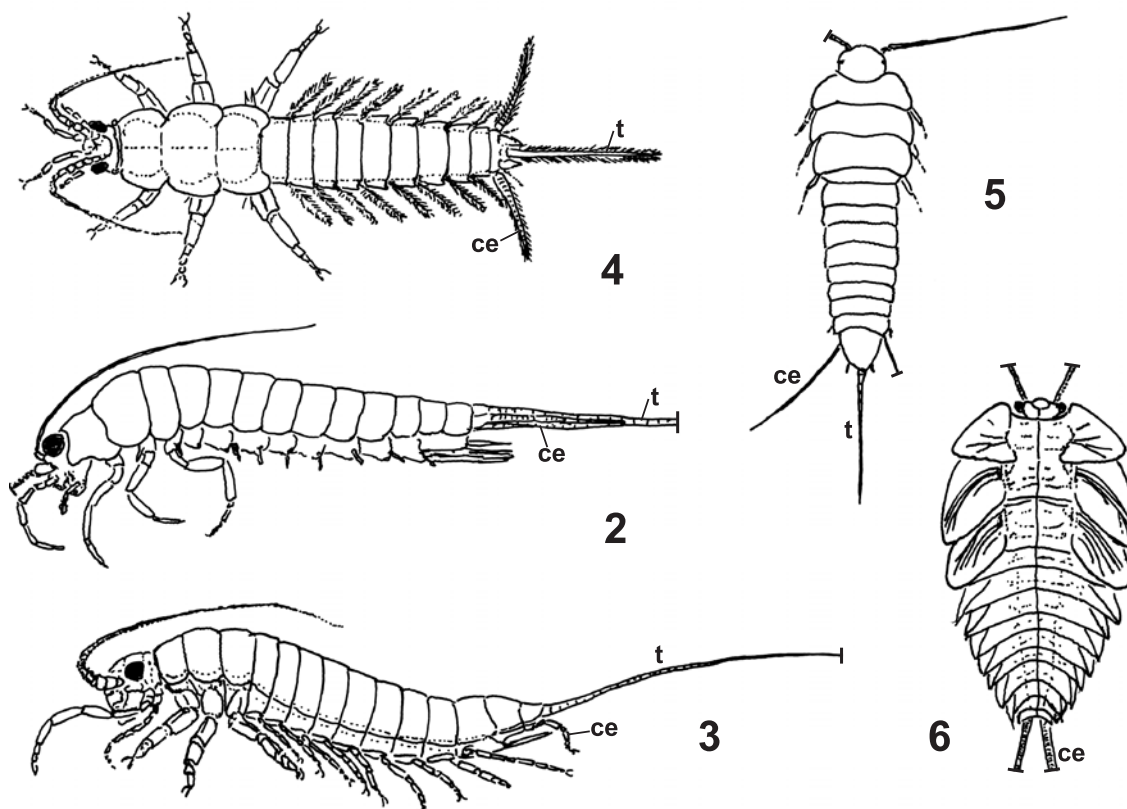
It was one of the further aims of the present work to discuss the transformations of the lepismatid mesothoracic structures into the pterygotan ones in more detail and to clarify how the most basal lepismatid subcoxa became integrated into the base of the ventral wall of the wing (section 2.3.). It was already assumed by RASNITSYN (1981) that the wings are composed of both paratergal and pleural parts. This is in accordance with the observations that during the pterygotan ontogeny the wing buds appear firstly remote from the terga in the pleural region and migrate later to the tergum (TOWER 1903; KUKALOVÁ-PECK 1978).

Another problem treated herein is the differentiation of the complicated wing articulation. This depends on the answer of the question: were the wings initially palaeopterous (i.e., unable to flex the wings rearwardly on the back) or did the flexing ability (i.e., neoptry) evolve almost simultaneously with the sustained flight? Nearly all authors accept the Palaeoptera hypothesis. But BRODSKY (1970) and RASNITSYN (1981) found that all elements of wing flexing are already present in the Ephemeroptera supporting the view that the neopterous state may be a groundplan feature of all Pterygota. WILLKOMMEN & HÖRNSCHEMEYER (2007) added further evidence. I tried therefore to understand the structure of the wing articulation as the result of very early flexing ability of the evolving wings (sections 2.4.–2.5.3.).

Finally some ecological and functional aspects are discussed which followed the acquisition of flight (section 2.6.).



**Fig. 1.** Cladogram of the basal Ectognatha indicating the sequence of the main events on the way to insect flight.



**Figs. 2–6.** Typical representatives of basal Ectognatha showing important characters; ce – cercus, t – terminalfilum. **2:** *Machilis* spec. (Archaeognatha). **3:** “*Dasyleptus*” (Monura): Carboniferous, reconstruction (redrawn after KUKALOVÁ-PECK 1987). **4:** *Ramsdelepidion schusteri* Kukulová-Peck, 1987: Upper Carboniferous, reconstruction (redrawn after KUKALOVÁ-PECK 1987). **5:** *Lepisma saccharina* Linnaeus, 1758. **6:** Young palaeodictyopteran nymph: Upper Carboniferous (redrawn after KUKALOVÁ-PECK 1978).

## 2. The evolutionary way to insect flight

Fig. 1 shows the well founded cladogram of basic Ectognatha with the main acquisitions important for the evolution of insect flight. There are three important steps. The first occurred already at the base of Ectognatha in a common ancestor of Archaeognatha and Dicondylia with the evolution of the terminalfilum and the special features of the flagellate antennae. These are autapomorphies of Ectognatha missing in the non-ectognathan Hexapoda.

### 2.1. First step of mastering the air

The Archaeognatha, which are represented by the extant Machilidae and Meinertellidae, have moncondylous mandibles with which the animals are able to scrape off loose food material. The machilids are living in the assemblages of rock fragments at the base of both sea shore (*Petrobius* spec.) and inland rocks (*Dilta* spec., *Machilis* spec.). They hide between the stones and feed small algae and lichen particles growing on the upper surface of the stones. For escaping predators and for locomotion they are able to execute high jumps of approximately 1 dm distance (MANTON 1972; EVANS 1975). Backward and forward jumps are equally possible. Characteristics of the skeleto-muscular system of the thoracic legs indicate that the forward force component in forward jumps must be generated by the forceful backward movements of the thoracic legs (I. Hasenfuss unpubl. observations).

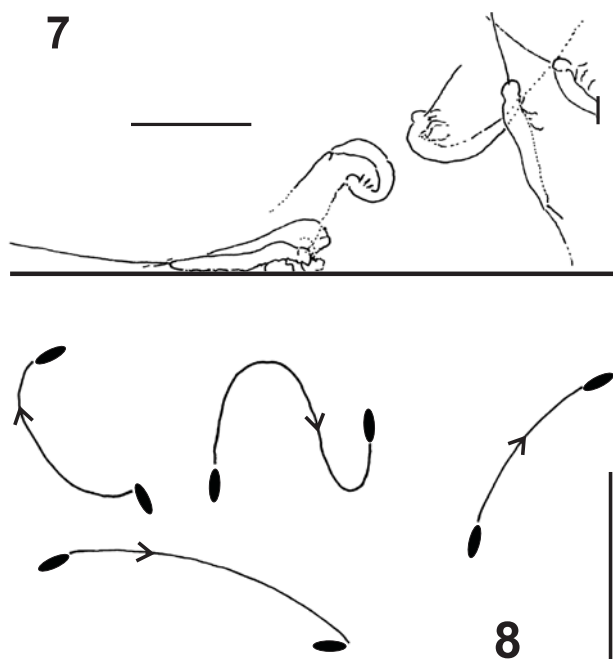
The take off was already analyzed by EVANS (1975) with high speed cinematography showing that the animal very rapidly curls the thorax ventrally and push the abdomen against the ground. Then it makes a somersault before it attains a horizontal attitude. To study how it stops the rotation I photographed the take off in the light of a self-made stroboscope (Fig. 7). After approximately 25 ms the anterior body part is extremely curled and 25 ms later it is already straight again. During this time the antennae are moved from the back to the front in prolongation of the body length axis and then backwardly again. Uncurling the body, the movements of the antennae and the laterally outstretched legs reduces the rotation so much that the animal attains a horizontal attitude with the head in direction of the jump.

The terminalfilum is an annulated median, comparatively stiff bristle-like projection of the last (11th) abdominal tergite (Fig. 2). Its role became apparent

by observing the jump trajectories which could be followed with the unaided eye. The terminalfilum is not only engaged in stopping the rotation but also in steering the course of the jumps. The animals are able to jump from the ground to the side or the top of stones and can execute horizontally curved jumps (Fig. 8). Horizontal curves are possible by sidewardly bending the body. The thorax is dorsally somewhat convex, laterally compressed, and the paratergites are bent downwards and form thus vertical planes which can be utilized for horizontal steering (Fig. 2). Amputation of the terminalfilum has the result that the animal is unwilling to execute jumps, and if it does, the jumps are uncontrolled, erratic. In the course of the next one or two moults the terminalfilum is fully regenerated. These observations demonstrate the importance of the terminalfilum for mastering the air. This structure is generally maintained in Dicondylia except for Metapterygota (Figs. 1, 4–5). The cerci (ce in Fig. 2) are originally abdominal legs that are modified to annulated filiform appendages and support the function of the terminalfilum. Accordingly, they lost their active intrinsic movability.

Another important acquisition in this context is the altered construction of the antenna. Originally, the antennal segments are moved against one another by intrinsic muscles. In contrast to this, the ectognathan antennae are built of only three segments: scapus, pedicellus and the slender annulated flagellum. Pedicellus and flagellum are only passively movable to one another. Both are movable as a unit in all directions by muscles within and at the base of the scapus. The antennae do not only help to control the body attitude but are also specialized for the perception of air currents. The scolopal organs within the pedicellus (Johnston's organ) had replaced the formerly present muscles and permit the perception of fluttering of the flagellum caused by air streams, regardless if during jumps, falling down or flight. This construction of the antennae is thus universally suitable and hence generally maintained in Ectognatha.

A further adaptation is the peculiar trunk musculature. The rapid curling and subsequent stretching of the body demand longitudinal and oblique muscles with extreme and fast contraction capacity. As is shown in Fig. 9, this is attained by joining the initially separated muscles together to compact ventral and dorsal cords in which the contracting fibrils are twisted (MANTON 1972; BIRKET-SMITH 1974). The peripheral fibrils shorten the muscle not only by their own contraction but additionally by the pull caused by thickening of the centrally located muscle fibrils as a result of their contraction. Furthermore, the contraction of the whole muscle complex is accelerated. If this muscular organization was likewise realized in the ancestor of Ectognatha, then the muscles must have been restored to



**Figs. 7, 8.** High jumps of Machilidae (Archaeognatha). **7:** *Machilis* spec.: forward jump drawn from a photograph made with a selfmade stroboscope; time intervals 12 ms. (Scale bar: 10 mm) **8:** *Dilta* spec.: sketches of observed trajectories seen from above with unaided eyes. (Scale bar: 8 cm)



**Fig. 9.** *Petrobius* spec.: micrograph, histological celloidine-paraffin cross section through the 7th abdominal segment, 33  $\mu$ m thick, stained with Weigert's hematoxyline; ventral (v) and dorsal (d) complexes of twisted longitudinal and oblique muscles; arrows point to the location of the axes of concentricity. (Scale bar: 0.1 mm)

the usual construction with more parallel fibrils when the jumping ability was given up in the branch leading to Lepismatidae and Pterygota. In these taxa the muscles are not twisted.

The shape of the body, the terminalfilum and the characteristics of the antennae appear thus to be adaptations in the context of the machilid jump. Jumping should have begun as an erratic escape reaction from predator attacks (as in the Collembola with a completely different jumping mechanism), and the controlled jumps were doubtlessly adaptations to the life in the rock fragment assemblages. Controlled jumping is for this life style by far the best mode of locomotion. It permits to get quickly on the upper sides of stones for feeding and hence is maintained up to now. There are no doubts that the machilid jumping ability evolved already in the ancestor of Ectognatha and that attitude control of the body was the first step in mastering the air.

## 2.2. The acquisition of the dicondylous mandible, early fossil Dicondylia and the role of vascular plants

Another important event was the formation of the anterior articulation of the mandible, the autapomorphy of the Dicondylia. It was initially of the gliding type, which is described by VON LIEVEN (2000) and STANICZEK (2000). This type is present in early Dicondylia including Ephemeroptera among the Pterygota (Fig. 1). In all other Pterygota the ground plan of the anterior articulation is of the advanced, very effective socket-ball type, one of the principal autapomorphies of Metapterygota. Both types permitted to bite off small particles from hard compact material and allowed the exploitation of vital vascular plants, especially the nutritious tips of the shoots with their growing tissue and generative organs.

Spores from terrestrial, probably liverwort-like plants are known already from the mid Ordovician and megafossils of Tracheophyta are known from the late Silurian (WELLMAN et al. 2003). The early vascular land plants were of *Rhynia* type with slender, vertical, leafless, some dm high stems standing in groups and ending in sporangia. Climbing and the exploitation of plant tips is well documented by coprolites containing vegetative tissue fragments and undigested spores from the late Silurian and early Devonian (EDWARDS et al. 1993; LABANDEIRA 2006). This palynivory is the oldest type of plant damage by hexapodes.

According to the reconstruction of "*Dasyleptus*" by KUKALOVÁ-PECK (1987), the extinct Monura were Dicondylia with the anterior mandible articulation

of the gliding type, small fully articulated abdominal legs which seem to be adapted for climbing up the thin stalks of early land plants, a long slender terminalfilum, and leglike cerci (Fig. 3). The last point suggests that the filiform annulated cerci in Machilidae and Cercofilata evolved independently to assist the function of the terminalfilum. However, WILLMANN (2003) doubts whether all fossil specimens used for the reconstruction belong to the same group and whether all mentioned characters, especially the leglike abdominal appendages including the cerci, are really monuran ones. The thorax of Monura was dorsally convex as in Machilidae, and this may indicate that the Monura were still able to jump and that this ability was likewise a groundplan feature of Dicondylia.

### 2.2.1. The origin of lepismatid organization

Another fossil reconstructed by KUKALOVÁ-PECK (1987) is *Ramsdelepidion* with lepismatoid features but with well developed eyes and (except for cerci) still small fully articulated laterally extending abdominal legs (Fig. 4). The articulation of the abdominal legs may be – as in Monura – a sign that the animals still climbed on plants. But the other features are so similar to extant Lepismatidae that there are little doubts that they had the same functional abilities. To these features belong: (1) the dorsoventrally depressed body with laterally extending flat paratergites and (2) the long filiform now annulated cerci which are extending laterally in horizontal attitude. These features are characteristics of basal Cercofilata (KUKALOVÁ-PECK 1987). They can be regarded as adaptations to an altered strategy to avoid predation still maintained in the extant Lepismatidae: (1) hiding in flat crevices (e.g., under stones) into which predators could not follow and (2) fast running. The jumping ability was lost together with the thoracic dorsal convexity of the machilid jumping system, it is replaced by fast running, which seems to be more effective outside the assemblages of rock fragments. As shown experimentally for extant Lepismatidae by HASENFUSS (2002), the filiform cerci and the terminalfilum permitted landing on the feet when falling down. Additionally, the cerci and terminalfilum function as sensory organs, as indicated by their rich equipment with sensillae.

It was an idea of HINTON (1963) that landing on the feet and quickly running away to escape predators may have played a role in the early evolution of wings. In the early Devonian there was a rich fauna of spider-like arachnids without net making ability (Trigonotarbida – SHEAR & KUKALOVÁ-PECK 1990). They hunted the contemporaneous hexapods probably in the manner of lycosides. Falling experiments showed that spiders are likewise generally able to land on their

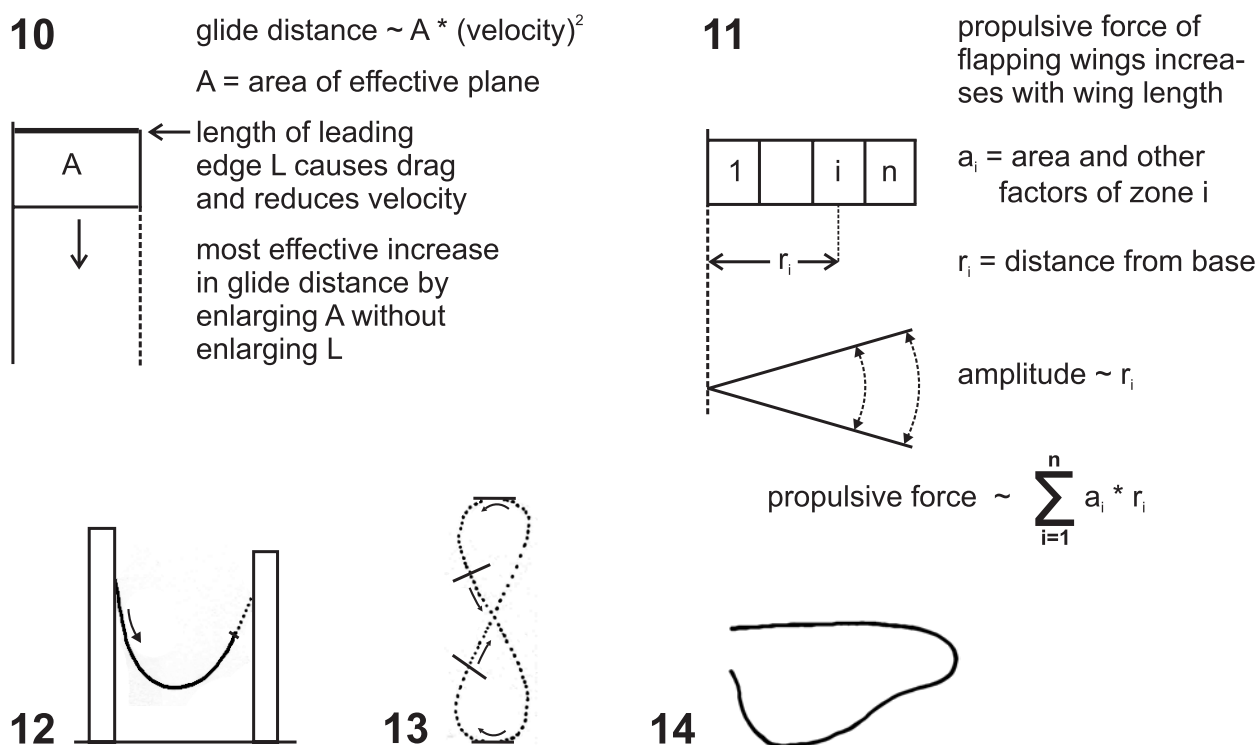
feet (HASENFUSS 2002). It was therefore possible that hunting was continued even when both the hunted and the hunter were falling on the ground from plants of low height. Running races between predators and their victims enhanced enormously the selection pressure because already tiny advantages of the hunted animal could be decisive for survival.

### 2.2.2. The gliding hypothesis

In this situation it could be advantageous to glide some distance away. Falling experiments with models of lepismatoid size and shape revealed their gliding ability if the cerci were still movable by muscles and could be put together after attaining the glide attitude. By this the animals got enough speed to glide some distance even when falling from low heights (e.g., 0.5 dm distance from 0.5 m height as shown by HASENFUSS 2002). As is explained in Fig. 10, the glide distance is proportionate to the square of velocity and the area of the effective plane. The leading edge causes drag and hence reduces velocity if it becomes elongated. Selection for glide distance favoured therefore large plane areas with short leading edges. This effect is confirmed by the glide experiments with different models (HASENFUSS 2002: IIB and IIC in fig. 8). Consistently, the initial lepismatid gliding ability could be increased by acquiring oval or oniscoid outlines of the body similar to those found in nymphs of Palaeodictyoptera (Fig. 6). It should be noted that soaring is quite different from gliding and should not be confused with it. Soaring utilizes updrafts of air and demands long wings with long leading edges creating high drag. The drag reduces both the forward speed and the sinking velocity and helps to keep the animal in the air during updraft breaks.

Extant Lepismatidae are, however, not able to actively move their cerci. But this may be an adaptation to their nocturnal life style with reduced eyes. Gliding without sight control can be disastrous, and the best possibility to escape predators is then to fall vertically down. It is therefore advantageous to keep permanently the cerci in the laterally extended position. In the lepismatid ancestors with well developed eyes and fully articulated abdominal legs it may well be that the filiform cerci retained their mobility by muscles and enabled thus gliding.

The main problem of the gliding hypothesis is, however, the transition from gliding to sustained flight with flapping wings. As it was pointed out by QUARTAU (1985), selection favouring glide distance did not favour sustained flight by flapping wings. Propulsive force could be created by flapping extensions when the leading edge was more rigid and the plane behind slightly deformable. Then each down-



**Figs. 10–14.** Physical aspects of wing evolution. **10:** Conditions for the increase of glide distance. **11:** Effect of wing length on propulsive force of flapping wings with stiff leading edge and passive pronation and supination during down- and upstroke, respectively. **12:** Evolutionary transition from gliding to active flight; wing flapping could only become effective when the glide velocity was reduced to zero, e.g., by flying upwards, caused by appropriate attitude of the caudal filaments. **13:** Trajectory of the wing tip of the most effective wing motions, view from the left, the arrows indicate the direction of movements. **14:** Broadened wing base indicates gliding components during flight.

stroke caused automatically pronation and each upstroke supination, and both caused backward thrust of air creating propulsive force. Some deformation is practically an unavoidable effect of wing beats even in modern insects. Initially only the propulsive force was needed because the body attitude was controlled by the caudal filaments and every desired lift component could be created by a suitable inclination of the pterothorax.

As shown in Fig. 11, the propulsive force caused by a transverse zone of the wing increases with the amplitude and this is proportional to the distance from the pivot point of the wing. The overall propulsive force increases with the wing length without altering the breadth of the wing. Further increase in propulsive force could be attained by backwardly moving the wings during the up- and downstrokes and by moving the wings forward when they are in the positions at the ends of the strokes. In combination with suitable pronation and supination the wing tips describe thus the well known 8-figure (Fig. 13). Basally broader wings are signs of utilizing glide phases during flight whereas the more slender terminal parts are more responsible for sustained flight (Fig. 14).

However, during gliding there is a rapid air stream from the front along the body. To be effective, the air-

stream caused by flapping extensions must be faster and this means faster than the glide velocity. The initially tiny protractive force of flapping extensions could only be of adaptive value when the forward speed was nearly zero. This was possible when the animal was falling down in a horizontal body attitude without gliding or when it was steering the glide path upwards and used the kinetic energy to gain height for landing on another stem (Fig. 12). In this case, even small additional propulsion could help to reach the next landing point on a neighbouring stem without the need to go down to the ground and climb again. The protractive force created by flapping wings could then be enlarged by selection.

The transition from gliding to sustained flight was therefore only possible by a change of the scenario in which descending from low height without delay and the increase of glide distance was no longer the predominant need. The ultimate reason for this could be the fact that during the Devonian some vascular plants became large trees. With increasing height, the horizontal deviation during falling became so great that escape from predators by gliding ceased to be an important factor and the change to another plant without descent and climbing again was much more important for the exploitation of the plant tips.

### 2.2.3. An alternative hypothesis without intermediate gliding

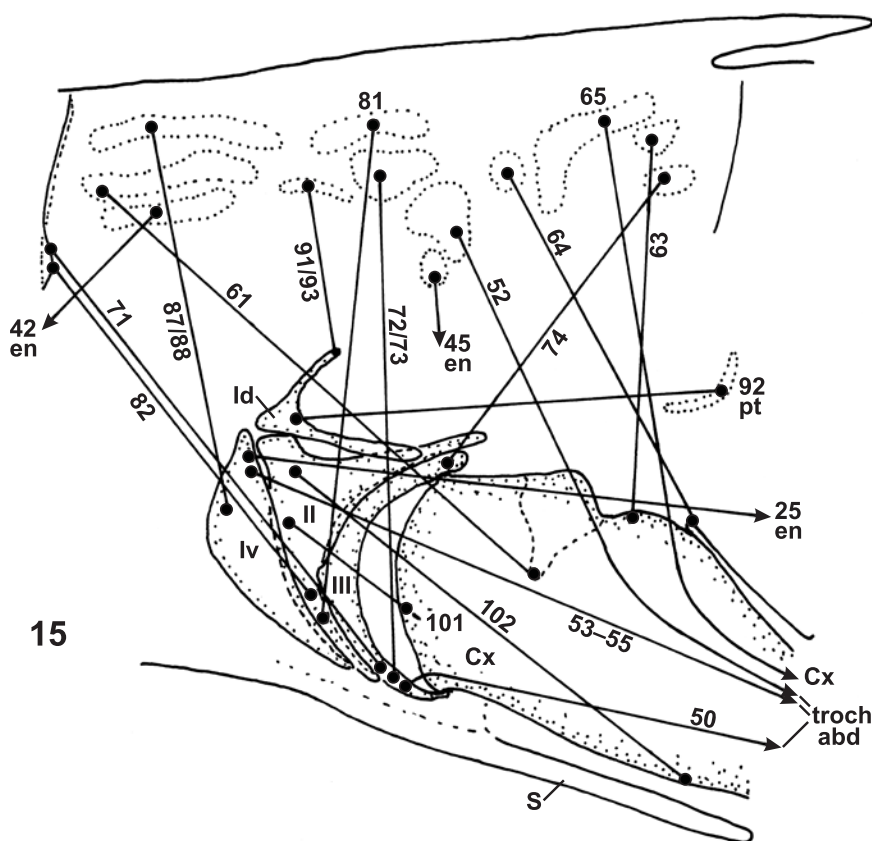
Unexpectedly, the re-examination of a pair of mandibles from the Under Devonian Rhynie Chert in Scotland proved that they are clearly of the metapterygotan type (ENGEL & GRIMALDI 2004). This means that at that time – when the land plants were up to 1 m high – there was already some radiation of flying insects suggesting that the wings evolved before the land plants were tall enough to permit effective gliding. A scenario without intermediate gliding should therefore be taken into account. As pointed out in the previous section, the precondition for acquiring flight with flapping extensions are situations in which the animal is in the air and the forward speed is nearly zero. Just this is the case when the animal flees from a predator and falls vertically down on the feet as is demonstrated by living lepismatids (HASENFUSS 2002). If the falling height is too low for gliding, even small propulsion by flapping extensions may help to escape. This hypothesis seems to be not less probable than the gliding hypothesis. It is much simpler than the latter. The assumption of both an intermediate gliding phase and a change of the scenario is superfluous, and the suitable scenario appeared long before the glide scenario. It was the first opportunity to evolve wings.

### 2.3. The transformation from lepismatid to pterygotan thoracic organization

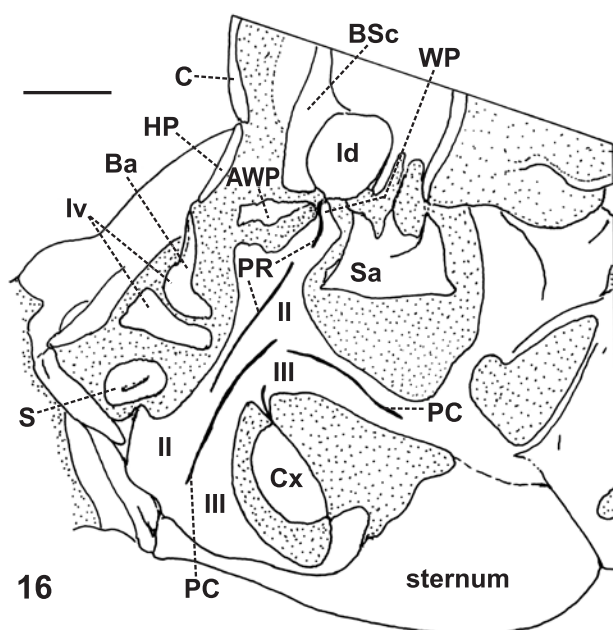
Whatever has happened, there is morphological evidence that the lepismatid thoracic organization was transformed into that of Pterygota. By comparing the functional morphology of the mesothorax of *Lepisma* with the pterothorax of Pterygota many homologies become apparent that permit to reconstruct the details of the transformation. The study of the mesothorax of *Lepisma* revealed anterodorsal sclerites of three subcoxal leg segments with articulations between one another and each with muscles of its own (Id, Iv, II, III in Fig. 15, and figs. 1–4 in HASENFUSS 2002). The most basal subcoxal sclerite is subdivided by a joint into a dorsal (Id) and an anteroventral (Iv) part for functional reasons. The complex of all these sclerites is surrounded by pleural membrane and is moved by muscles in antero-posterior direction to increase the stride length as an adaptation for fast running. Coxa and femur are flattened and appressed backwardly to the body, and this led to a drastically altered leg movement system by integrating all subcoxal leg segments. When the legs were appressed to the body the whole ventral side could act as an aerodynamically effective plane.

It should be noted that three subcoxal and six distal segments (coxa, trochanter, femur, tibia, tarsus and praetarsus) make up a total of nine leg segments, which might be, according to PAULUS (1985), the ancestral number in Euarthropoda. In early Euarthropoda, the legs were not only used for locomotion but also for food particle transport between the leg pairs towards the head, as is found in some Crustacea. This and the supposedly similar food uptake mode in the extinct Trilobita suggests that the very early marine ancestors of Euarthropoda gained food by walking on the rounded littoral rock fragments and scratched off the small organisms growing on the stones with their basal leg segments. After the food transport was omitted, the basal leg segments became modified or more or less reduced. But they did not disappear fully. In non-ectognathan Hexapoda, residual pleural sclerotizations are retained and known as anapleurite (I), katapleurite (II), and trochantinus (III). They bear mechanoreceptive sensillae indicating that these are still needed for the sensory system long after the leg segments in question had lost their other functions. Sclerotization stabilizes the basal rings of tactile setae forming thus a reference plane for the shaft when it is bent out of its resting position. The evaluation of the information from the mechanoreceptive sensillae by the central nervous system is apparently so complex that its reorganization is difficult and the system hence conservative. [Other examples of this principle are the thoracic coxal styli of machilids and the flagellum in Arachnoidea. When the scorpionid tail was no longer used for killing prey, it became short and stout, and the space of its former caudal extension became occupied by the flagellum, a filiform annulated tergal process of the last segment bearing the still necessary sensillae (retained in extant Uropygi). Only once the central nervous system was sufficiently reorganized, it was possible to omit the flagellum as well. It is quite similar to the ectognathan terminalfilum, but its evolutionary history is very different.]

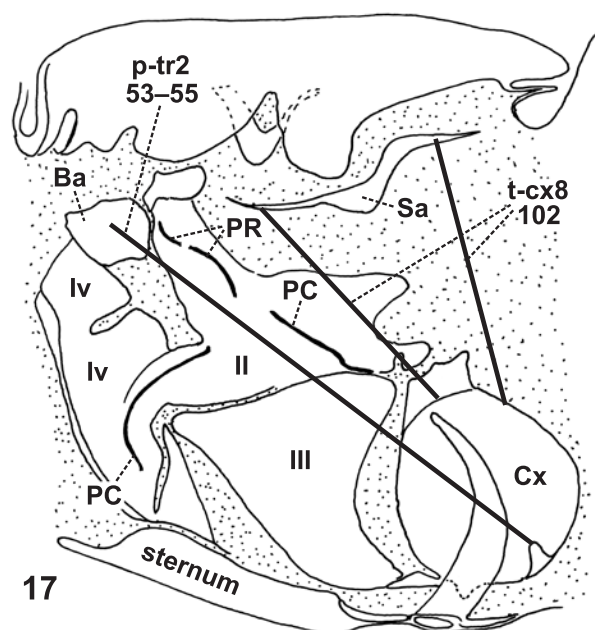
Starting from lepismatid organization, the paranota could have become movable simply by desclerotization along a narrow tergal zone above and slightly proximal from the articulation Id/II (uns in Fig. 18). Up and down movements of the paratergites were then possible by the muscles already present. Precondition were tensile internal connections between the dorsal and ventral cuticle of the paranota by fibrillary structures traversing both epidermis layers. Such fibrils are visible in histological sections of Lepismatidae (I. Hasenfuss unpubl. observations). There are numerous muscles in *Lepisma* which originate on the tergite and insert on each of the leg segments I, II, III, coxa and trochanter (Fig. 15). Their contraction could depress the tergite, and the ventral part of the articulation Id/II could work as a fulcrum for the upward



**Fig. 15.** *Lepisma saccharina*: mesothorax, lateral view, skeleto-muscular system of the leg base, paranotum omitted; arabic numbers – muscle names according to MATSUDA (1970); abd – abductors; muscle insertions on non-cuticular endoskeleton (en), paranotum (pt), trochanter (troch); s – sternum (after HASENFUSS 2002).



**Fig. 16.** *Ephemera vulgata* Linnaeus, 1758: mesothorax, left side, outer view; membranous cuticle dotted. (Scale bar 0.5 mm)



**Fig. 17.** *Periplaneta americana* (Linnaeus, 1758): exoskeleton of metathorax, internal view of right half, with muscles of basalare Ba and subalare Sa; membranous cuticle dotted; p-tr2, t-cx8 – names of muscles after MATSUDA (1970); arabic numbers – homologous muscles of *Lepisma* in Fig. 15 (redrawn after BRODSKY 1996).

movement of the paratergite (Fig. 18). Only few of the lepismatid muscles are needed for this movement. Contraction of the antagonistic tergal longitudinal and

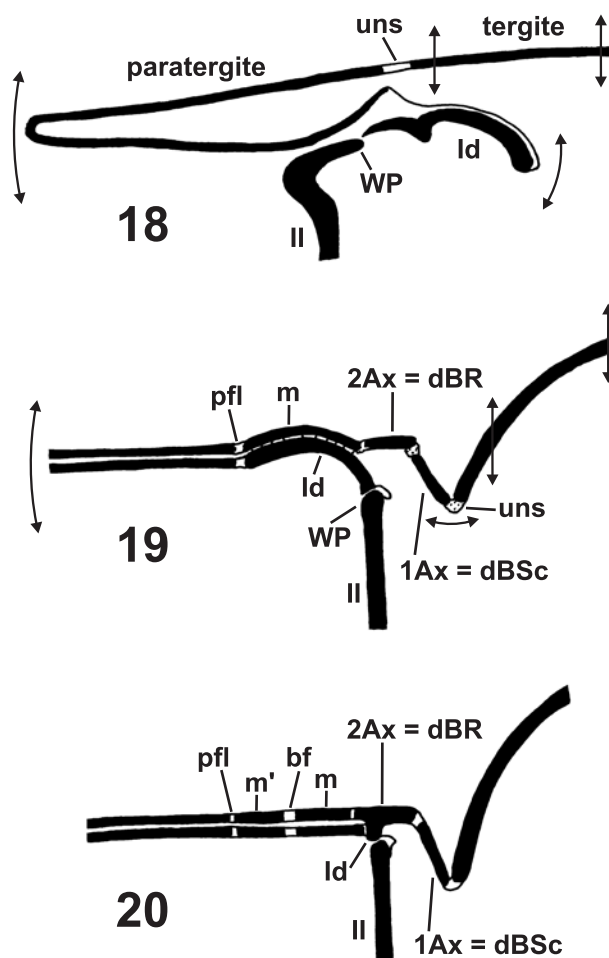
oblique muscles caused downstroke by arching the tergite lengthwise and thereby lifting its lateral margin above the articulation Id/II.

Homologies of the thoracic muscles in *Lepisma* and Pterygota are proposed by MATSUDA (1970) and HASENFUSS (2002: figs. 4, 10). The muscles inserting on pleural sclerites in Pterygota are originally leg muscles, and some of them are still bimodal, that is, used for both wing and leg movements (Fig. 17). Bimodal muscles with alternative different functions are of great advantage in flying animals because they help to minimize weight. The leg movement frequency is variable and goes up to approximately 50 Hz in the fastest fleet of Lepismatidae (MANTON 1972; HASENFUSS 2002). This suggests that – ab initio – the wing beat frequency could optimally be adjusted. It is in most insects within or near the range of 20 to 30 Hz (BRODSKY 1994) and thus well in the range of the leg movement frequency.

Since the leg base and with it the articulation Id/II was initially movable antero-posteriorly by muscles, effectiveness of the flapping paranota could be improved by holding the articulation firstly in place by muscles and later by integrating the subcoxae in a system of sclerotizations forming a rigid frame for the actions of both wings and legs. Numerous traces of this event are detectable in Pterygota, as it was pointed out by HASENFUSS (2002). Two additional examples are shown in Figs. 16 and 17, in which the regions of the subcoxal sclerites are still recognizable. The paracoxal suture (PC) and a more plesiomorphic stage of the pleural ridge (PR) mark the form of the subcoxa II. The advanced pleural ridge connects in a straight line the pleural wing process (WP) and the dorsal coxal articulation. It prevents bending of the pleural wall by the contractions of the dorsoventral muscles. The invaginated sclerite Id was turned outwardly and became part of the ventral wall of the wing, also bearing the articulation to the pleural wing process (WP in Figs. 19, 20).

## 2.4. The problem of wing flexion

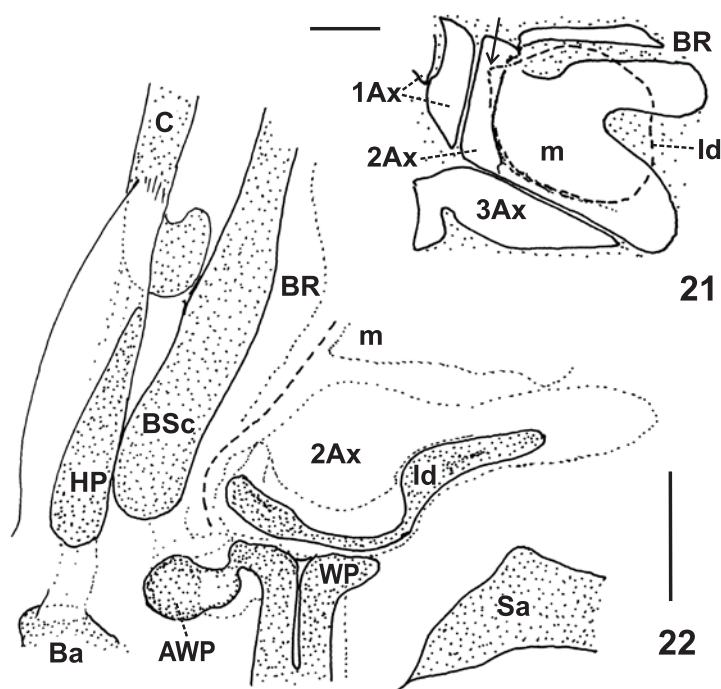
The further reconstruction of the evolution of the wing base depends from the answer to the question whether the wings were initially neopterous (i.e., capable of flexing or folding the wings on the back) or palaeopterous (unable to do this). Most authors assume the second possibility because many Palaeozoic fossil insects (Palaeodictyoptera with the exception of Diaphanopterodea) and the two more plesiomorphic extant pterygotan taxa – Ephemeroptera and Odonata – are unable to flex the wings. However, BRODSKY (1970, 1974) and RASNITSYN (1981) claimed that all elements of wing flexing are present already in Ephemeroptera. WILLKOMMEN & HÖRNSCHEMEYER



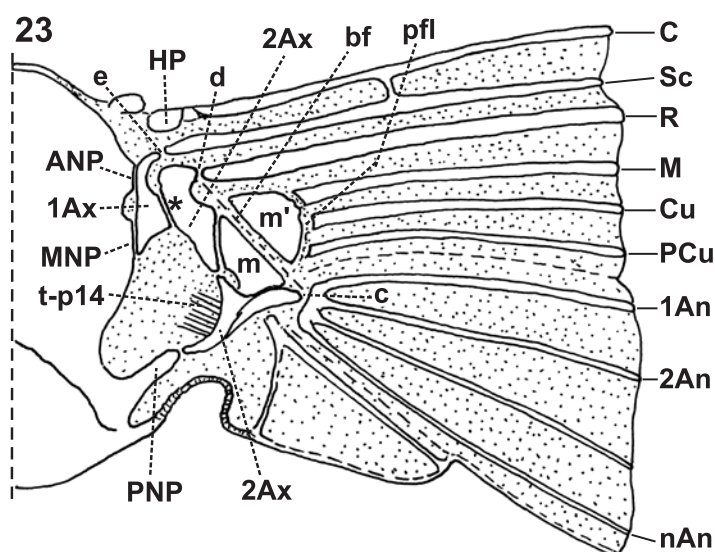
**Figs. 18–20.** Schematic cross sections through the paratergite/wing articulation in different stages of wing evolution. **18:** *Lepisma*. **19:** Pterygota with subimaginal moult. **20:** Pterygota with subimaginal moult omitted.

(2007) presented more arguments in favour of the neoptery hypothesis. Furthermore, this hypothesis is strongly supported by evolutionary considerations. When the evolving wings became elongated and laterally extended beyond the sides of the other paratergites, they conflicted with things in the environment when the animal was walking or running. By far the best solution of the problem was flexing the wings by turning them horizontally on the back.

Precondition for wing flexing was the development of a switch that permitted the clear separation of the two functional states, flight and non-flight. When in flight, the wings have to act as sufficiently stiff planes and flexing must be safely prevented by a locking mechanism. When the animal is walking or at rest, the wings should be flexed, horizontally turned backwards by suitably folding. As is already described by SNODGRASS (1935), the first stages of flexing are observable in freshly killed insects. Flexing occurs automatically by tensions within the cuticle when the muscle which causes the deflected state relaxes. The



**Figs. 21, 22.** Wing base. **21:** *Ephemera vulgata*: subimago, middle zone of the right mesothoracic wing, dorsal view; membranous parts punctured; the outline of the sclerite Id in the ventral wall of the wing is dashed, the arrow points to the wing articulation of Id below the axillary sclerite 2Ax; homologies of sclerites according to WILLKOMMEN & HÖRNSCHEMEYER (2007). (Scale bar: 0.2 mm) **22:** Wing articulation of *Tettigonia viridissima* Linnaeus, 1758 (Orthoptera), left metathoracic wing, ventral view; flexion line dashed, sclerites densely dotted; outlines of covered sclerites are punctured; Id is fused with 2Ax on the dorsal side. (Scale bar: 0.5 mm)



**Fig. 23.** Diagram of wing articulation, dorsal view. The asterisk shows the site of the ventral pivot point; membranous cuticle dotted, flexion lines dashed. ANP, MNP, PNP – anterior, median, posterior notal process, respectively; c, d, e – flexion line articulations within veins; t-p14 – flexor muscle (name after MATSUDA 1970); at the right – names of longitudinal vein stems (redrawn after SNODGRASS 1935).

corresponding skeleto-muscular mechanism activates alternatively the flexed and deflexed state. Both states could then be optimized simultaneously by selection on variations of the sclerotization and tension patterns within the cuticle in connection with adaptations of the muscular system.

## 2.5. Differentiation of the wings and the wing articulation

The differentiation of wings and their moving mechanism is an extremely complex event. Structures and

functions had to meet many requirements at the same time, among them: low weight, sufficient stiffness, adequate force transmission, flexion, supply with nerves and blood and at least initially the ability to moult. Low weight and stiffness was realized by the development of the veins in all paranota – as indicated by the fossil record even in the prothorax – on the basis of structures preformed already in Lepismatidae (ŠULC 1927; ANDER 1938). The veins contain blood lacunae, sensory nerves and tracheae, and the adjacent cuticle above and below is sclerotized thus forming a stiffening system. The general pattern of the basal stems of the branching longitudinal veins is shown in Fig. 23 in dorsal view. Supposedly they ended primarily within the membranous zone surrounding the wing base.

From the very beginning of the wing evolution there were two articulation systems present: the tergo-alar system at the base of the dorsal wall and the pleuro-alar system on the ventral side. The latter is based on the lepismatid articulation Id/II. The sclerite Id was turned outwardly and became part of the ventral wing wall articulating on the pleural wing process (WP in Fig. 19, 20). Generally it can be stated that the tergo-alar system was responsible for the force exertion on the flapping wings and that the role of the differentiations of the pleuro-alar system was the control of the different movements of the wings: especially pro- and retraction and pro- and supination as well.

As noted above, both articulation systems were ab initio braced together to a functional unit by tensile fibrils connecting the dorsal and ventral cuticle of the wing. The fibrils permit ecdysis and connected especially sclerite Id – after it was turned outwardly – with the dorsal cuticle. The area above Id became the median plate (m in Figs. 19, 20, and m/m' in Fig. 23). Imaginal ecdysis is retained in Ephemeroptera, and in these the sclerite Id evolved to a conspicuous rounded concave sclerite (Figs. 16, 21). Its size and dome-like shape allowed tight connections between Id and m and reduced drastically the deformability of both (Fig. 19). Id articulates with the pleural wing process WP at a point located a bit proximal from the median plate and below the dorsal sclerite 2Ax (arrow in Fig. 21).

After the omission of the imaginal moult in non-ephemeropteran Pterygota the ventral sclerite Id and the dorsal axillary sclerite 2Ax fused to a rigid unit by cuticular connections traversing the interior of the wing. The former fibrils connecting Id with the median plate and the large size of Id were no longer necessary. Sclerite Id became reduced to an elongated and curved narrow strip in the ventral corner of the wing (Figs. 20, 22), while the more lateral parts became unsclerotized. It should be noted that the omission of the imaginal moults permitted the degeneration of the epidermis in the wings and thus minimized mass and energy needed for flight. Measurements revealed that the thickness of the imaginal wing in *Ephemera vulgata* is approximately half of that of the subimaginal wing (I. Hasenfuss unpubl. data). Nevertheless, the Ephemeroptera retained the imaginal moult; the possible reasons for this are discussed in MAIORANA (1979).

The m-Id complex, articulated with the pleural wing process WP, was the basic part of the wing which fundamentally influenced the pattern and organization of the other sclerotizations, especially the bases of the longitudinal veins between which it became integrated.

### 2.5.1. The pleuro-alar system of articulations

With the development of the unsclerotized dorsal strip uns in Fig. 18 there was ab initio a need to stabilize the anterior wing margin with its costal vein (C in Fig. 23). The problem was solved by a tensile connection with the dorsal end of the sclerite Iv. The costa was therefore not free for wing beat force transmission. The connection became the humeral plate (HP in Figs. 16, 23), and the adjacent dorsal part of Iv became the basalare (Ba in Figs. 16, 17). The basalare was hinged to the remainder of Iv so that contraction of its muscles turns it inwardly and pulls the wing forward and into a pronated inclination. The homology of the basalare with the dorsal part of the lepismatid Iv is obvious especially from the presence of a bimodal muscle extending to the trochanter (compare Figs. 17 and 15). The basalare mechanism seems to be the switch that permitted the initiation of wing flexing. Tension of its muscles keep the wing in a deflexed state. This is indicated by the observation that in extant insects flexion begins automatically when these muscles (and those which evolved later in supporting deflexion) relax.

As is shown in Fig. 22, the sclerotization of the ventral base of the subcosta (BSc) is very conspicuous and forms a loose articulation with the rigid anterior arm (AWP) of the pleural wing process (WP). AWP is the former anterodorsal part of the lepismatid sclerite II. Between BSc and Id there is a flexion line which is in the flexed state deeply invaginated, and this explains why there is no distinct ventral base of vein R. The articulation BSc/AWP is the main articulation for wing flexion; it permits turning the anterior margin of the wing rearwards on the lateral side of the body. In *Ephemera*, the AWP is still present as a residual sclerite, and the BSc became closely applied to Id (Fig. 16). The absence of the ventral R-sclerotization and the presence of AWP in *Ephemera* is a sign that the inability to flex the wings is secondary and that wing flexion is suppressed (among other changes) by the rigid connection of BSc with Id.

There is little doubt that the subalare (Sa in Figs. 16, 17, 22) is a detached movable part of the dorsal margin of the lepismatid sclerite II. Behind WP, it has a tensile connection with the sclerite Id, and more posteriorly it is connected with a sclerite which appears to be the ventral sclerotization of the common base of the anal veins. The contraction of the subalar muscle pulls the posterior part of the wing base downwards and cause thus supination, a very important component of wing movements. The subalare is the antagonist of the basalare mechanism. [As noted above, the basalare causes pronation simultaneously with the deflexed state of the wing.] It seems that the contraction of the subalar muscle likewise supports the deflexed state by

pulling the point c in Fig. 23 downwards. This point is raised during flexion (see 2.5.3.).

The resulting degree of wing inclination depends on the degree of the tensions of both the basalare and subalare muscles. Whether the contraction of these muscles creates additionally down- or upward movements depends on the location of their dorsal attachment in relation to the point of wing articulation. They cause upstroke if the muscle attachments of both sides are closer together and downstroke if they are more lateral. Pronation of the wings by the basalare mechanism is combined with protraction. The observed rearward movement of the wings is still to be analyzed.

MATSUDA (1970: 69) regards the subalare to be a detached part of the tergite. He bases this notion on findings that the subalare muscle (his t-cx 8) “arise from the tergum, when the wing is absent or weakly developed”. He thinks that the muscle is the homologue of a tergo-coxal muscle in *Lepisma* which originates far in the anterior half of the tergum. But the main subalare muscle is inserted on the dorsal margin of the coxa. It is an old bimodal muscle already present before the evolution of wings began, and it is difficult to imagine how the tergal sclerite could have reached its definite pleural position below the wing during the evolutionary process. The pattern of sclerites suggests that the subalare is much more likely a detached posterior part of sclerite II and that the muscle is the homologue of 102 in *Lepisma* (compare Figs. 17 and 15). As a functionally important leg muscle it needed a firm dorsal attachment before the wing anlagen in the juvenile stages became differentiated. It was therefore shifted on the tergite for functional reasons and this attachment does not indicate the evolutionary origin of the corresponding dorsal sclerite.

## 2.5.2. The tergo-alar articulations

In the first evolutionary stages, the dorsal bases of the longitudinal veins were doubtlessly extending to the primary zone of weakness (uns in Fig. 18). The bases of veins M, Cu, and PCu fused and formed the median plate above the sclerite Id (m in Figs. 19–21 and m/m' in Fig. 23). The sclerotizations of the veins in the dorsal wall, the fixed WP and the margin of the tergite form a lever system which transmits the deformations of the tergites caused by the flight muscles into up and down movements of the wings. The effect of the deformations was improved by forming the initially flat tergite to a vault with downwardly extending lateral margins (compare Figs. 18 and 19). This caused a deep furrow at the wing base and led to laterad movements of the middle zone of the tergal margin when it was lifted by the contraction of the longitudinal tergal muscles. The reverse happened when the antagonists

were in action. The lateral movements had to be compensated for by a movable nearly vertical intermediate sclerite between the tergal margin and the dorsal wing wall (Figs. 19, 20).

For functional grounds, the lateral margins of the tergites had always to be rigid and could not be the source of a movable part. This problem and the problem of exerting force on the anterior wing part was solved by parallel rearward extensions of the dorsal basal stems of both the subcosta and radius (dBS<sub>c</sub> = 1Ax and dBR = 2Ax, respectively, in Figs. 19 and 23). The extension dBS<sub>c</sub> formed a hinge with both the anterior notal process (ANP) and the median notal process (MNP), which are arranged symmetrically to the pivot point. The membranous strip between dBS<sub>c</sub> and dBR was utilized as a hinge nearly parallel or oblique to the former (compare Figs. 19 and 23). This explains why both bases extended rearwardly between the median plate (m) and the margin of the tergite and not the Sc alone. The dBS<sub>c</sub> became the movable axillary sclerite 1Ax, and Sc+1Ax forms a characteristic arch around the base of vein R and its rearward extension, the axillary sclerite 2Ax. Sclerite 1Ax became movable by the articulation e in Fig. 23, whereas 2Ax remained in the wing plane. The hinge 1Ax/2Ax and the articulation e permit variable angles between 1Ax and the wing plane. This allows not only compensation for the sideward movements of the tergal margin but also the transmission of force on both the Sc and the 2Ax (Fig. 23). Sclerite 2Ax is responsible for the functionally very important lever proximal from the pivot point of the wing.

The articulations d and c in Fig. 23 are part of the flexing system and are locked during flight. The veins C, Sc and R are close together and braced by cross-veins or fusions. All forces exerted on one of these veins influence the movement of the whole complex and hence the anterior margin of the wing. Behind the median plate m, the bases of the anal veins fused to the sclerite 3Ax, which was closely applied to m; it retained its articulation with the tergite (the posterior notal process PNP) and became articulated with 2Ax (Fig. 23).

A similar configuration of the dorsal bases of Sc, R/2Ax, of the median plate M/Cu/PCu and of the fused anal veins as described and shown in Fig. 23 is well recognizable in both a drawing of a nymph of Tchirkovaeidae/Palaeodictyoptera (KUKALOVÁ-PECK 1983: fig. 23) and a diaphanopterid (RASNITSYN 1981: fig. 8).

## 2.5.3. The wing flexing system

A stage in which the dorsal sclerotizations of the longitudinal veins were directly articulated to the margin of the tergite could have existed only at the very begin-

ning. As discussed above, the articulation between the humeral plate (HP) and the costa (C) on the one side and the articulation between 1Ax and the remainder of vein Sc on the other are to be regarded as adaptations for functional needs. The evolution of the flexing system began with increasing wing length, and led to a second line of weakness laterally to the wing articulation. This line separated basal sclerites from the longitudinal veins behind the Sc and permitted to turn the wing backwards in horizontal position. The general morphology and the folding process are well described in SNODGRASS (1935).

The evolving flexion line separated the axillary sclerite 2Ax from vein R at the point d in Fig. 23 and 3Ax from the anal veins at point c. As long as the imaginal moults were retained, the flexion line had to run distally in an arch around the median plate (pfl in Figs. 19, 23). This must be postulated because it was important to maintain the sclerite Id and hence the median plate rigid. This explains why the median plate (m and m') has a rounded shape. Whether articulation d in Fig. 23 was already part of the primary flexion line is unclear; it may be that the line ran more distally. After the omission of the imaginal moult and the size reduction of sclerite Id, a secondary line was introduced between the points d and c (bf in Fig. 23). It divided the median sclerite into the two parts m and m' and functions as a hinge which is raised dorsally and becomes strongly convex in the flexed state. This acquisition permitted more rigid connections of m' with the distal veins and improved thus the stability of the wings. The triangular shape of the axillary sclerite 3Ax, with its apical articulation c and the basal articulations 3Ax/PNP and (3Ax + m)/2Ax, offered the possibility to improve wing flexing by turning sclerite 3Ax on the back, together with the attached sclerite m. The initial step of flexion is caused by cuticular tension and moves the insertion point of the axillary flexor muscle (t-p14 in Fig. 23) at a point dorsad and mesad from the basal articulations. This is possible because the insertion is located in a crotch of the sclerite. The origin of the muscle is located at the wing process WP and the muscle contraction fixates the wing in the flexed position on the back of the animal. All these changes were possible because the sclerotization on the ventral side of the vein Sc stabilized the anterior wing margin ab initio in full length. Generally, deflexion is apparently possible not only by protracting the wing with the basalare mechanism but also by pulling the hinge m/m' downward with the subalare apparatus.

The Ephemeroptera retained the imaginal moult and, accordingly, their median plate is undivided. Fig. 21 shows the situation of the subimago. In the definitive imago, the median plate is enlarged, distally more rounded, and the dorsal base of R is fused with the anterior part of the median plate m.

The present hypothesis offers the simplest and most parsimonious explanation of the pteralia which is well in accordance with the permanent selection pressure on flying animals to reduce weight as far as possible. In contrast to this, KUKALOVÁ-PECK (1983) assumes an ancestral band of no less than four rows each with eight pteralia which she thinks is needed for the interpretation of wing base surface structures in the fossils of Palaeodictyoptera.

## 2.6. Ecological and functional aspects following the flight ability

After the acquisition of flight in the pterygotan branch, the small abdominal legs of early Dicondylia lost their role for climbing plants and became reduced. Since the ecological zone of exploitation of plants was occupied by the ancestors of Pterygota and climbing on plants was no longer sensible in the ancestors of extant lepidismatoids, the articulated abdominal legs were likewise reduced.

With increasing height of vascular plants, the vast majority of flying insects became arboricolous and fed as adults mainly on plantal branch tips. Once the flying ability was so improved that the mature insects were – in contrast to nymphs – able to fly from plant tip to plant tip without much walking, the flexing ability lost its significance and was reduced independently several times in Palaeozoic insects, especially the Palaeodictyoptera (WILLKOMMEN & HÖRNSCHEMEYER 2007). The Diaphanopterodea are clearly members of Palaeodictyoptera, but they were able to flex the wings. The discussion on the nature of this neoptery is controversial. KUKALOVÁ-PECK (1978) thinks that palaeoptery is primary and regards neoptery in Diaphanopterodea and Neoptera as the result of parallel evolution, whereas RASNITSYN (1981) does not find principal differences to the other neopterous insects. A more recent example are the Papilionoidea among the Lepidoptera which – after the appearance of angiosperms – were adapted to fly from flower to flower in a special flight mode with very broad wings (BRODSKY 1994). These independent events, and the freedom in optimizing the special flight modes without consideration for the flexing mechanism explains the great diversity in the patterns of wing base sclerotizations of “palaeopterous” insects. Neoptery is much less variable, which can be regarded as a sign of its common origin.

The damage by insects with initially biting mouth parts caused protective adaptations especially in trees (e.g., mechanically by enclosing the soft parts in hard, lignified covers) and these led to altered feeding strategies. The exploitation of branch tips could be main-

tained by adapting the biting mouth parts to piercing-sucking ones that could penetrate the protective devices of the plants. This was realized by the many-fold Palaeozoic Palaeodictyoptera with their typical autapomorphic proboscis (KUKALOVÁ-PECK 1985: fig. 33). Since herbaceous plants have less possibilities to protect themselves mechanically – they utilize other strategies like fast growth, short vegetation periods, colonizing new sites, etc. – insects with biting mouth parts could well exist when they became in all stadia ground dwellers which fed on herbaceous living plants (as, e.g., Orthoptera) or dead plant material (as Blattodea). Both mentioned taxa realized life modes which are nearly identical in all postembryonal stadia, with the exception that the adults have special tasks like dispersion by flight, propagation, etc. This strategy was apparently the basis for the vast majority of extant insects.

Unlike modern adult Ephemeroptera, the adult Palaeozoic Ephemeroptera had well developed biting mouthparts (KUKALOVÁ-PECK 1985) but we know nothing about the food uptake. Giving up food ingestion permits the utilization of the alimentary system for other purposes. The ingestion of air into the gut in the extant Ephemeroptera allows effective nuptial flight by stabilizing the long abdomen and reducing weight. Dancing males execute forward vertical upward flight during which the cerci are put close to the terminalfilum. This is followed by parachuting with spread caudal filaments. To begin the upward flight, the abdomen is bend dorsally and the caudal filaments are used to attain vertical posture of the body. The terminalfilum is still useful and therefore retained in some Ephemeroptera. In other Ephemeroptera only the movable filamentous cerci are retained as in some other insects, e.g., Plecoptera and the Palaeozoic Palaeodictyoptera. The other Pterygota do not utilize the caudal filaments as devices for attitude control, this task is taken over by the wings.

The adaptive zone of flying carnivorous hunters became occupied by Odonata. Grasping other insects in flight with the legs demanded special adaptations and caused the extreme reorganization to the odonatan flight apparatus. It can be regarded as the result of selection that favoured the ability to turn the legs in the flight direction and to concentrate the wing articulations close together at a point shifted posteriorly as far as possible. This caused the oblique arrangement of the pterothoracic segments enabling the legs to be used as effective grasping devices (“Fangkorb”). The exertion of force on the wings was taken over by the muscles which originally controlled the finer wing movements, and this permitted to reduce drastically the size of the tergites between the wings. The wings became located at the posterior margin of the pterothorax. Apart from grasping prey the legs were mainly used for sitting and

less for walking between vegetation. Wing flexion became therefore unimportant and caused no constraints in optimizing the flight apparatus. Moreover, when the wings are put together dorsally they do not protrude much because they are directed posterodorsally due to the backward inclination of the pterothorax. Since the hunter had to be larger than the hunted, a possibility to reduce mortality by predation was to increase the body size, and this may have led to an evolutionary race in size between hunters and their prey. This may explain the observed gigantism among the Palaeozoic insects. The wingspan of the largest known fossil odonatan insect was ~ 0.7 m, and that of a member of Palaeodictyoptera ~ 0.5 m (ELLINGTON 1991). No other flying hunters were present during the Palaeozoic.

### 3. Summary and Conclusions

Studies on the jumps of Machilidae revealed that the filiform annulated terminalfilum as well as the 3-segmented ectognathan antennae with their long annulated filiform terminal segment evolved as a means of body attitude control already in the archaeognathan stage on the evolutionary way to Pterygota. The scolopidia of Johnston’s organ became means to percept the vibrations of the terminal antennal filament caused by the airstream along the body initially during jumps and later when falling down or in flight. With the formation of the anterior articulation of the mandibles, at first as a gliding mechanism and later as the ball-and-socket construction typical for Metapterygota, the early Dicondylia were enabled to bite off small particles from compact hard material. Exploitation of the growing plant tips and generative organs (palynivory) became possible by climbing up plant shoots. Fossil coprolites and the small but fully articulated abdominal legs of early Dicondylia support the view that this was really the case. Whereas the extinct Monura seem to have retained the jumping ability, the Lepismatoidea changed the survival strategy against predators. They were adapted for very fast running and hiding in flat crevices into which predators could not follow. Predators enhance the selection pressure because small advantages of the hunted may be decisive for survival. When the lepismatoid animals fell down they landed on the feet, and the ventral plane was large enough to permit gliding. Both abilities could possibly be useful in escaping predators (e.g., spider-like Trigonotarbidia in the early Devonian).

Flapping protowings could only be effective when the speed in the anterior direction was nearly zero. This

could happen when the height of the plants increased so that landing on a neighbouring shoot became more important. By steering the glide path upwards, the kinetic energy could then be used to gain height. Protractive force by flapping extensions could then help to attain a landing point. If the plants were not high enough, there was chance for the evolution of flapping extensions when the insect attained horizontal attitude when falling down without intermediate gliding.

The regions of the three subcoxal thoracic sclerites and some of their muscles in *Lepisma* are still recognizable in Pterygota. The dorsal articulation between the (subdivided) most proximal and the following leg segment is transformed into the wing articulation. The dorsal part of the proximal segment (Id) is integrated into the system of the ventral vein sclerotizations of the wing. After omitting the subimaginal ecdysis it fused with the axillary sclerite 2Ax on the dorsal side by cuticular connections traversing the interior of the wing. The notion that neoptery, i.e., the ability to flex or fold the wings on the back, was primary is strongly supported by evolutionary considerations. When walking or running, the elongating wings soon conflicted with things in the environment. The best solution of the problem was the nearly simultaneous differentiation of the wing articulation system and wing flexion (i.e., the folding of the wings horizontally on the back). This was possible by a mechanical switch that alternately separated the states of flexing and flight. This switch is apparently the basalare mechanism: the contraction of its muscle protracts and deflects the wing whereas its relaxation initiates flexion. The line of flexion separated, on the dorsal side, basal portions of the longitudinal vein sclerotizations. Whereas the base of subcosta may have become movable as the axillary sclerite 1Ax for other reasons, 2Ax and 3Ax seem to be detached from the corresponding veins by the flexion line. The bases of media, cubitus and postcubitus fused to the median plate as the dorsal counterpart of sclerite Id. The ventral sclerotization of subcosta forms a loose articulation with the anterior arm of the pleural wing process (i.e., the pivot point of the wing). This articulation permits turning the wing backwards for flexion.

## 4. Acknowledgments

I am grateful to Klaus-Dieter Klass and Niels Peder Kristensen for giving me the occasion to present my results on the 3rd Dresden Meeting on Insect Phylogeny. Furthermore, I thank the editor Klaus-Dieter Klass for the editorial work and useful critical remarks.

## 5. Abbreviations

1Ax, 2Ax, 3Ax	axillary sclerites
Id, Iv, II, III	lepismatid subcoxal sclerites, corresponding regions in Pterygota
AWP	anterior arm of pleural wing process
Ba	basalare
bf	secondary flexion line crossing the median plate
BR	base of radius
BSc	base of subcosta at underside of wing
C	costa
Cx	coxa
dBR	detached base of radius
dBSc	detached base of subcosta
HP	humeral plate
m, m/m'	median plate
PC	paracoxal suture
pfl	primary flexion line distal from the median plate
PR	pleural ridge
R	radius
S	spiracle
Sa	subalare
Sc	subcosta
uns	hypothetical line of weakness between paratergite and tergite
WP	pleural wing process

## 6. References

- ANDER, K. 1938. Die neue Auffassung über die Tracheisation des Insektenflügels. – *Opuscula Entomologica* **3**: 83–90.
- BIRKET-SMITH, S.J.R. 1974. On the abdominal morphology of Thysanura (Archaeognatha and Thysanura s.str.). – *Entomologica Scandinavica, Supplementum* **6**: 1–67.
- BRODSKY, A.K. 1970. Organization of the flight system of the mayfly *Ephemera vulgata* L. (Ephemeroptera). – *Entomological Review, Washington* **49**: 184–188.
- BRODSKY, A.K. 1974. Evolution of the wing apparatus in the Ephemeroptera. – *Entomological Review, Washington* **53**: 25–43.
- BRODSKY, A.K. 1994. *The Evolution of Insect Flight*. – Oxford University Press, Oxford, New York, Tokyo, 229 pp.
- EDWARDS, D., P.A. SELDEN, J.B. RICHARDSON & L. AXE 1993. Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. – *Nature* **377**: 329–331.
- ELLINGTON, C.P. 1991. Aerodynamics and the origin of insect flight. – *Advances in Insect Physiology* **23**: 171–210.
- ENGEL, M.S. & D.A. GRIMALDI 2004. New light shed on the oldest insect. – *Nature* **427**: 627–630.
- EVANS, M.E.G. 1975. The jump of *Petrobius* (Thysanura, Machilidae). – *Journal of Zoology, London* **176**: 49–65.

- FLOWER, J.W. 1964. On the origin of flight in insects. – *Insect Physiology* **10**: 81–88.
- HINTON, H.E. 1963. The origin of flight in insects. – *Proceedings of the Royal Entomological Society of London (C)* **28**: 24–27.
- KINGSOLVER, J.G. & M.A.R. KOEHL 1985. Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. – *Evolution* **39**: 488–504.
- KINGSOLVER, J.G. & M.A.R. KOEHL 1989. Selective factors in the evolution of the insect wings: response to KUKALOVÁ-PECK. – *Canadian Journal of Zoology* **67**: 785–787.
- KLUGE, N.J. 1989. A question on the homology of the tracheal gills and paranotal processi of mayfly larvae and the wings of insects with reference to the taxonomy and phylogeny of the order Ephemeroptera. – *Lecture series in memory of N.A. Kholodkovsky* **41**: 42–77. [in Russian]
- KUKALOVÁ-PECK, J. 1978. Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. – *Journal of Morphology* **156**: 53–126.
- KUKALOVÁ-PECK, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. – *Canadian Journal of Zoology* **61**: 1618–1669.
- KUKALOVÁ-PECK, J. 1985. Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera). – *Canadian Journal of Zoology* **63**: 933–955.
- KUKALOVÁ-PECK, J. 1987. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). – *Canadian Journal of Zoology* **65**: 2327–2345.
- KUKALOVÁ-PECK, J. & C. BRAUCKMANN 1990. Wing folding in pterygote insects, and the oldest Diaphanopteroidea from the early Late Carboniferous of West Germany. – *Canadian Journal of Zoology* **68**: 1104–1111.
- LABANDEIRA, C. 2006. Silurian to Triassic plant and hexapod clades and their associations: new data, a review, and interpretations. – *Arthropod Systematics & Phylogeny* **64**: 53–94.
- LIEVEN, A. VON 2000. The transformation from monocondylous to dicondylous mandibles in the Insecta. – *Zoologischer Anzeiger* **239**: 139–146.
- MAIORANA, V.C. 1979. Why do adult insects not moult? – *Biological Journal of the Linnean Society* **11**: 253–258.
- MANTON, S.M. 1972. The evolution of arthropodan locomotory mechanisms. Part 10. Locomotory habits, morphology and evolution of the hexapod classes. – *Journal of the Linnean Society of London, Zoology* **51**: 203–400.
- MARDEN, H.J. & M.G. KRAMER 1994. Surface-skimming stoneflies: a possible intermediate stage in insect flight evolution. – *Science* **266**: 427–430.
- MARDEN, H.J. & M.G. KRAMER 1995. Locomotor performance of insects with rudimentary wings. – *Nature* **377**: 332–334.
- MARDEN, J.H. 2003. The surface-skimming hypothesis for the evolution of insect flight. – *Acta Zoologica Cracoviensia* **46**: 73–84 (suppl.).
- MATSUDA, R. 1970. Morphology and evolution of the insect thorax. – *Memoirs of the Entomological Society of Canada*, No. 76, Ottawa. 431 pp.
- MATSUDA, R. 1981. The origin of insect wings (Arthropoda: Insecta). – *International Journal of Insect Morphology & Embryology* **10**: 387–398.
- PAULUS, H. 1985. Euarthropoda. Pp. 768–791 in: R. SIEWING (ed.), *Lehrbuch der Zoologie, Band 2 Systematik*. – Gustav Fischer Verlag, Stuttgart.
- QUARTAU, J.A. 1985. On some objections to the paranotal theory on the origin of the insect wings. – *Boletim da Sociedade Portuguesa da Entomologia, Suplemento* **1**: 359–371.
- QUARTAU, J.A. 1986. An overview of the paranotal theory on the origin of the insect wings. – *Publicacoes do Instituto de Zoologia 'Dr. Augusto Nobre' Faculdade de Ciencias do Porto* **194**: 1–42.
- RASNITSYN, A.P. 1981. A modified paranotal theory of insect wing origin. – *Journal of Morphology and Physiology* **168**: 331–338.
- RASNITSYN, A.P. 2003. On the skimming hypothesis of the origin of insect flight. – *Acta Zoologica Cracoviensia* **46**: 85–88 (suppl.).
- SHEAR, W.A. & J. KUKALOVÁ-PECK 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. – *Canadian Journal of Zoology* **68**: 1807–1834.
- SNODGRASS, R.E. 1935. *Principles of Insect Morphology*. – Cornell University Press, Ithaca and London. 667 pp.
- STANICZEK, A. 2000. The mandible of silverfish (Insecta: Zygentoma) and mayflies (Ephemeroptera): Its morphology and phylogenetic significance. – *Zoologischer Anzeiger* **239**: 147–178.
- ŠULC, K. 1927. Das Tracheensystem von *Lepisma* (Thysanura) und die Phylogenie der Pterygogenea. – *Acta Societatis Scientiarum Naturalium Moraviae* **4**: 1–344. [in Czech with German summary]
- TOWER, W.L. 1903. The origin and development of the wings in Coleoptera. – *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* **17**: 517–572.
- WELLMAN, C.H., P.L. OSTERLOFF & U. MOHIUDDIN 2003. Fragments of the earliest land plants. – *Nature* **425**: 282–285.
- WIGGLESWORTH, V.B. 1963. The origin of flight in insects. – *Proceedings of the Royal Entomological Society of London (C)* **28**: 23–24.
- WIGGLESWORTH, V.B. 1976. The evolution of insect flight. In: R.C. RAYNEY (ed.), *Symposia of the Royal Entomological Society of London* **7**: 255–269.
- WILLKOMMEN, J. & T. HÖRNSCHEMEYER 2007. The homology of wing base sclerites and flight muscles in Ephemeroptera and Neoptera and the morphology of the pterothorax of *Habroleptoides confusa* (Insecta: Ephemeroptera: Leptophlebiidae). – *Arthropod Structure & Development* **36**: 253–269.
- WILLMANN, R. 2003. Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme. – *Verhandlungen Westdeutscher Entomologentag 2001, Düsseldorf*: 1–64. [In German]

