A possible evolutionary pathway to insect flight starting from lepismatid organization

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Abstract

Starting from the hypothesis that flight in Pterygota evolved from lepismatid organization of their ancestors, the functional anatomy of the thorax was studied in *Lepisma saccharina* Linnaeus, 1758, and a *Ctenolepisma* sp. in regard to both the adaptations to the adaptive zone of Lepismatidae and to pre-adaptations for the evolution of Pterygota. Well-preserved parts of three subcoxal leg segments were found in the pleural zone participating in leg movement. The lepismatid strategy of escaping predators by running fast and hiding in narrow flat retreats led to a dorso-ventrally flattened body which enabled gliding effects when dropped, followed by flight on the ground. The presumed exploitation of soft tissue at the tips of low growing Devonian vascular plants opened a canalized pathway to the evolution of the flying ability. Locomotion to another plant was facilitated by dropping. It is possible that threat by spider-like predators favoured falling and gliding as escape reactions by selection. Falling experiments with 'lepismatid' models revealed a narrow 'window' for gliding, with optimum dimensions of 8 mm body length and 8 mg weight. An equation was derived which describes the glide distance as function of weight, area of the horizontal outline, the specific glide efficiency of the body, and a non-linear function of the falling height. Improved gliding was made possible by enlarging thoracic paratergites into broad wing-like extensions of light-weight organization. The disadvantage of the lateral lobes for locomotion on the ground of a membranous strip between tergite and horizontally when gliding. This movability could be attained by the intercalation of a membranous sterip between tergite and the utilization of the most basal subcoxa was thus integrated into the wing. Initiation of active flight was possible by flapping movements during gliding. Morphological, ontogenetic and ecological aspects of the origin of Pterygota are discussed.

Key words: functional anatomy - locomotion - evolution - flight - Lepismatoidea - Pterygota - regeneration

Introduction

Evolution, apart from phenomena of neutral evolution, can be regarded as a succession of adaptive solutions to problems with which consecutive generations of organisms were confronted. The solutions are always based on the previously achieved organization, including the ontogenetic potentialities of varying the organizational features. The adaptations are realized by alterations which are continuously favoured by selection within the limitations of environmental and organizational constraints. The correct reconstruction of the main aspects of evolutionary events depends largely on information about the ancestral precursor organization, especially on insight into its complex structural and functional relations. There is a good chance of adequate reconstruction if the plesiomorphic organization is well maintained in cladistically related organisms. The corresponding traits of these can then be reliably assigned to the ancestor in question.

There are no doubts that the cladistically nearest relatives of Pterygota are the Zygentoma as represented by the extant Lepismatoidea (see Hennig 1969; Kristensen 1975, 1981). The lepismatid organization is formed by the corresponding adaptive zone and according to Hennig's 'Deviationsregel' (Hennig 1953) it is probable that the preflight ancestor of Pterygota was likewise of this organization and inhabited the same adaptive zone. This hypothesis is especially justified if traits of this organization can be regarded as pre-adaptive for the evolution of flight and if one or other of the pterygotan features can be traced back to specific lepismatid adaptations.

The conclusion is almost inevitable, if the Zygentoma are paraphyletic in terms of Pterygota as taken into account by Boudreaux (1979) and Staniczek (2000). The relict *Tricholepidion gertschi* Wygodzinsky (1961) (Lepidotrichidae) has maintained the ligament between the transversal mandibular muscles typical for the basal insect lineages, whereas in both the other Zygentoma and Pterygota the ligament has disappeared and the corresponding muscle insertions shifted partly to the anterior tentorial arms and partly to the hypopharynx (see Staniczek 2000 for discussion). Recently, Fürst von Lieven (2000) and Staniczek (2000) found that the larvae of Ephemeroptera retained the lepismatoid mandible working mechanism (in the imago the mouth parts are atrophied) and that both the Odonata and the Neoptera are in this respect synapomorphous and constitute the monophylon Metapterygota. This contributes additional support to the assumption that Pterygota evolved by transformation from a lepismatid stage.

The aim of the present work was to study and understand the features of the lepismatid organization as adaptations to the corresponding adaptive zone and to find an evolutionary pathway to pterygotan organization with the aid of an appropriate hypothetical scenario. It seems sound to argue that from all thinkable hypotheses about a historical evolutionary process that one will come next to the real event which is most conclusive, namely, which explains a maximum of observable evolutionary results, found in fossil or extant organisms, by necessitating a minimum of speculative assumptions. A scenario which meets these conditions as far as possible is presented.

It was necessary to study the structural and functional features of the skeleto-muscular system of the lepismatid thorax on preserved and living specimens because the existing references do not satisfy the demands of this work. The description of the skeleto-muscular patterns by Barlet (1951, 1953, 1954) does not permit insight into the movements that actually occur and the analysis of the locomotory system by Manton (1972) is, at least for the basal parts of the legs, not detailed enough. As pointed out by Ellington (1991) all aerodynamic theories postulate some form of gliding as the first step in the evolution of flight. Falling and gliding

experiments with models offered the opportunity to obtain information on the aerodynamic potentialities of lepismatid insects as the presumed starting point for the evolution of active flight.

Materials and methods

The morphological, functional and behavioural studies were made on *Lepisma saccharina* Linnaeus, 1758, captured in my home, and on an undetermined *Ctenolepisma* species from Tenerife living outdoor under stones. The latter species was sampled by lifting stones and holding them above a plastic film, the disturbed animals soon dropped down and were not able to run away on the smooth film. The captured animals were either fixed and preserved in a mixture of 2-propanol, acetic acid and formaldehyde recommended by Smith (1970) or held alive for months in glass vials with cork stoppers that were moistened daily. The vials contained some crumpled paper and little food (rolled oats, dry catfood).

The spatial relationships of the pterothoracic skeleto-muscular system were studied in both thick sections made with a razor blade and in complete series of histological sections. The thick sections were faintly stained with diluted picro-indigocarmine, embedded in cedarwood oil and examined microscopically, partly with polarized light and a first-order-red compensator plate. The histological sections were stained with Cason's trichrome (see Böck 1989), a simple modification of Mallory's triple stain which enables discrimination between endocuticle, mesocuticle and exocuticle. The numbering of muscles are according to Matsuda (1970).

The movements of the cuticular parts during leg-moving cycles were studied on living specimens where the dorsal side was stuck to a small metallic plate. The very rapid leg movements were observed visually with a stereo microscope and documented with flash-light photography (see Fig. 3A–C); the series of phographs permitted the reconstruction of the different phases of movement. The maximal number of leg moving cycles per second was estimated from stride length and the maximal running speed. The speed was roughly estimated by comparison with reference speeds and the stride length was measured from the distance between footprints left on a smoky glass plate.

The postures and attitudes of freely falling animals were photographed in the light of a digital stroboscope (Novadirect, Kehl, Germany) with 194 flashes per second against a remote dark background.

The gliding abilities of lepismatid insects were tested by experiments with models imitating the insects in shape, horizontal outline and mass. The models were cut out of stiff paper or thin cardboard, and the mass was adjusted by sticking suitable pieces of metal to the underside of the 'thorax' (see Fig. 6). They were either used as 'flat' models or stuck with suitable pieces of foamed plastic to imitate the spatial shape of *Lepisma* more closely (see f in Fig. 6b). Finally, the models were bent in a fashion for optimal gliding. Starting from size and mass of living

Lepisma (body length L = 8 mm, planform area A = 12 mm², weight 8 mg), models of different size were made by isometric variation. The models were dropped from various heights H and the glide distance X was measured on the ground as the distance between the landing point and the point below the point of falling. Each experiment was repeated n = 20 times. For details see legends to Figs 6–8 and Tables 1 and 2.

Results and discussion

Lepismatid adaptive zone and organization

The lepismatid adaptive zone is characterized by the combination of two strategies to avoid mortality by predators. (1) Seeking refuge in narrow flat spaces (e.g. below stones) into which predators cannot follow. (2) Running away as fast as possible when disturbed or when in the open. The corresponding selection caused extreme fleetness and a dorsoventrally flattened, extremely smooth and lithe body with backwardly directed flattened thoracic legs (Figs 1 and 3A). The effectiveness of these strategies is obvious from the fact that in Tenerife, for example, abundant populations of a *Ctenolepisma* sp. coexist with the small gecko *Tarentola delalandii* Dumeril & Bibron, 1836, in the same habitat.

That living or refuge-seeking within flat spaces is an ancestral feature of all extant Lepismatoidea (i.e. Lepismatidae, Nicoletiidae and Lepidotrichidae) is obvious from the peculiar form and posture of the palpus labialis which is the same in all Lepismatoidea. For reasons of space, the palpus is curved backwards behind the mouthparts and ends in a widened, dorso-ventrally flattened terminal segment (Fig. 3A). In Nicoletiidae, the body is less dorso-ventrally flattened than in Lepismatidae, apparently because the Nicoletiidae are secondarily subterraneous. Lepismatidae are especially well-adapted to flat spaces: the posterior sternal border bears a flange overlapping and protecting the basal median part of the coxae (s in Fig. 3A). The sternal flange is missing in both the Nicoletiidae and the Lepidotrichidae (see Wygodzinsky 1961).

Subcoxal parts

Adaptation to life in flat spaces resulted in a uniquely organized skeleto-muscular system of the thorax, as shown in Figs 1–4 for the pterothorax of Lepismatidae. The present studies led to the conclusion that there are three distinct subcoxal leg segments proximal to the coxa in spite of the fact that these segments are only antero-dorsally sclerotized; the

Table 1. Glide distance X of nearly isometric, flat lepismatid models of different size

Model size	Ι			II			III			IV		
L	4 mm			8 mm			16 mm			32 mm		
A	3 mm^2			12 mm^2			50 mm ²			200 mm ²		
М	2 mg			8 mg			65 mg			500 mg		
	X	SD	max	X	SD	max	max X SD max X SD	SD	max			
Glide distance (cm)	11.2	7.2	23	39.1	15.4	59	19.9	11.3	37	10.3	4.5	19
Glide distance (cm)	14.5	11.5	31	45.3	10.1	58	20.6	6.8	32	10.5	2.1	14
Glide distance (cm)	-	-	-	50.1	11.2	65	21.6	7.1	30	-	-	-
Glide distance (cm)	-	-	-	~53.5	~6.3	~62	26.8	5.2	33	-	-	-
Expected X (cm)	45			45			23			12		

Definition of L, A, M and the models' shape and posture as in Fig. 6. The values of L, M, A of model size II are the same as in adult Lepisma saccharina. The models were dropped from height H = 1.9 m, the 'head' pointing downward. Each mean X is the result of 20 glide experiments with the same individual model; SD, standard deviation; max, maximal value (all in cm). In the series marked with $\tilde{}$ only straight or nearly straight flights were taken into account. The expected values of X were calculated by using the formula in Fig. 6 and the constant $F \times f(H) = 300$ (mg/mm).

Table 2. Glide distances and estimated relative glide efficiencies of a type IIB model (Fig. 8) with plastic foam added, straight 'abdomen' and stepwise shortened 'wing length' (*WL*). Models were dropped in gliding orientation from height H = 1.0 m

В	WL	A	M	X	*F	*F'	Χ'
4	0	20	11.3	0.237	134	126.8	0.224
6	1	26	11.8	0.244	111	117.3	0.258
8	2	32	12.2	0.271	103	107.8	0.283
12	4	44	13.0	0.325	96	93.5	0.316
16	6	56	13.9	0.254	63	69.7	0.280
20	8	68	14.7	0.250	54	50.7	0.253

B, total breadth in the 'thoracic' region (mm); *WL*, wing length (mm); *A*, area of horizontal outline (mm²); *M*, mass (mg); *X*, measured glide distance (m), each value is the mean of n = 20 experiments;

* $F = F \times f(H)$, relative glide efficiency (g/m) for H = 1.0 m, estimated with the equation in Fig. 6;

 $F' = F' \times f(H)$, expected relative glide efficiency for H = 1.0 m, estimated from the linear regression $F' = 93.5 - 4.76 \times (B-11)$ with best fit to the experimental data; X' = expected glide distance estimated

arched sclerites are separated by infolded arthrodial membrane (Figs lc, 2, 3E,F, 4b). The surrounding pleural side wall and the posterior sternal parts of the segments are membranous. The subcoxae, or their sclerites, are marked here as I, II and III, beginning with the most basal one. For functional reasons discussed below, the most basal subcoxal sclerite is subdivided by a narrow joint into a dorsal and a ventral part (Id and Iv in Figs lc, 4b).

The sclerites I, II and III are known in the literature as anapleurite, catapleurite and trochantin, respectively. The assumption that the pleura and part of the sternal area are derived from basal leg segments is an old idea. However, it is normally thought that only one – or at most two – subcoxal segments are integrated (for review see Matsuda 1970; Boudreaux 1979; Kukalová-Peck 1983, 1987). The view that there are three subcoxal segments is supported by the following facts. (1) Each subcoxal sclerite has muscles of its own, one insertion is on the sclerite itself, the other either on a body part (tergite, endosternum) or on another leg segment (Fig. 4b). (2) Within each joint, there is at least one articulation between the sclerites (Fig. 1c). As described below, the whole subcoxal complex is moved together with the coxa; the leg base is freely movable within the membranous sidewall of the body. (3) The subcoxal sclerites and the basis of coxa are somewhat telescoped. All these parts bear groups of proprioceptive setae ventrally near their proximal margin suggesting serial homology (Fig. 2). It should be noted in passing that three subcoxal and six distal segments (coxa, trochanter, femur, tibia, tarsus



Fig. 1. Mesothoracic legs of *Ctenolepisma* sp. (a,b) and *Lepisma saccharina* (c–g), double headed arrows indicate possible movements. (a) Lateral view. (b) Dorsal view of leg. (c,d) Movability of coxae, covered contours dashed, membranes punctured. (e) Articulation III/cxv. (f). Articulation III/cxv. (g) Articulation III/cxv. (g) Articulation III/cxv. (g) Articulation III/cxv. (g) Articulation II/III. a–a', b–b', axes of rotary movements; p–p', parasagittal plane; Id, Iv, II, III, subcoxal sclerites; Id/II, II/III, III/cxd. (III/cxv. articulations; cx, coxa; fe, femur; pta, pretarsus; ti, tibia; tr, trochanter; ta, tarsus

by using $X' = *F' \times A/M$.



and pretarsus) make up a total of nine leg segments which might be, according to Paulus (1985), the ancestral number of Euarthropoda.

Leg movements

The transformation to backwardly directed legs necessitated considerable reorganization of the leg movement system. The observed movability of the more distal leg joints is shown in Fig. la,b. The propulsive backstroke occurs now by abduction of the trochanter, the forward stroke by its adduction (instead of remotion or promotion of the coxa, respectively).

The very fast leg movements were studied by a series of photographs made with flash light (Fig. 3A–C). In the photographs, the phase of the leg movement cycles could be identified by the known features of hexapodan leg coordination. According to Manton (1972), the legs of both sides of a segment normally work in opposite phase and the phase difference or time delay of succeeding legs is one-third of the pace duration. The relative durations of forward and back-strokes of each leg are approximately in the ratio 2 : 1, and the propulsive backstroke of a leg terminates nearly at the point when the leg behind has finished its forward stroke and started the backstroke.

Three main movements of the basal leg parts were observed. (1) Latero-median abduction and adduction of the coxae already described by Manton (1972) – different phases of movement are shown in Fig. 3A,B. (2) The leg base is moved anteriorly during the forward stroke (right body side in Fig. 3B) and posteriorly during the backward stroke (left body side). (3) Rotary movements on the longitudinal axis of the Fig. 2. Lepisma saccharina, antero-ventral view of left side metathoracic leg base showing subcoxal sclerites (Iv, II, III), coxa (cx), groups of proprioceptive setae (arrows) and muscle insertions. Covered contours are dashed or punctuated, for numbers of muscles see Fig. 4. III/cxv – ventral articulation of coxa

coxa. The lateral margin of right coxa is turned ventrally in Fig. 3C whereas it is lifted in Fig. 3B.

Movement (2) contributes to the stride length and thus improves the running speed. Movement (1) helps to keep the leg tip at the same comparatively short distance from the sagittal plane of the body – a fact which is indispensable for walking. The coxae of both body sides are simultaneously adducted to the median when the legs are in the middle of forestroke or backstroke (see forelegs in Fig. 3A). The coxae spread laterally when the legs are moved out of this position in anterior or posterior directions. The coxae move back to the median when the reverse occurs. The rotary movement on the longitudinal axis of the coxa is responsible for lift and touch down of the leg tip as described below.

Skeleto-muscular system of the pterothorax

Latero-median abduction of coxae must be caused by the contraction of muscles 101 and 102 (Figs 3 and 4b; i.h in Fig. 3E,F), adduction by muscles connecting the lateral margin of coxae with the endosternite (n in Fig. 3E, omitted in Fig. 4). The leg base is moved slightly backwards during the propulsive backstroke of the leg by two muscles inserting on the sclerites of subcoxa I: muscle 92 and the large muscle 25 (Fig, 4b; e.f in Fig. 3E,F). Lever effects between the anterior sclerite Iv and and the dorsal sclerite Id are avoided by a narrow membranous zone between both. (According to the present hypothesis that both belong to subcoxa I, this joint must be a secondary adaptation.) Sclerite Id is a flat triangular structure with thickened anterior margins, it occupies the bottom of a flat horizontal invagination (Fig. 3E,F). Poster-



Fig. 3. (A–C) *Ctenolepisma* sp. ventral side, flash photographs during 'rapid running', phases of leg movement. A, Overview. B, C, Metathorax. D, *Ctenolepisma* sp., micrograph of the mesothoracic trochanter, dorsal view, polarized light with first-order-red compensator plate. E, F, *Lepisma saccharina*, micrographs of histological cross sections of the left side of metathorax: E, overview, F, region of subcoxal articulation Id/II (F); large arrow points at the articulation Id/II; small arrow points at the tendon which connects muscle 53–55 with the dorsal end of sclerite Iv; for muscle numbers and for location of section planes see Fig. 4b (a-a' for E, b-b' for F). Id, II, III, subcoxal sclerites; ab, abductores trochanteri with cuticular tendon; ad, adductores trochanteri; ar, coxo-trochanteral articulation; cr, crop; cx, coxa; ec, endocuticle; fe, femur; mc, mesocuticle; p, paratergite; pl, palpus labialis; t, tergite; tf, trochantero-femoral muscles; tr, trochanter; s, sternal flange. Scale: 0.1 mm. Muscles of E, F: a, longitudinal medio-dorsal; b, longitudinal latero-dorsal; c, 91/93; d, 61; e, 92; f, 25; g, 53–55; h, 102; i, 101; j, 72/73; k, 81; m, longitudinal ventral; n, coxo-endosternal extending to lateral coxal margin; o, 71; q–31

iorly, it offers a place for the insertion of muscle 92 which originates within the paratergite (Fig. 4a,b; e in Fig. 3E,F).The invagination of Id is doubtless the result of the dorso-ventral depression of the body and was possible because the lateral longitudinal muscles above the invagination prevented conflicts with the dorso-ventral muscles (Figs 3E and 4a). The opposite movement during the forestroke is executed mainly by contraction of the muscles 61 and 31. Muscle 61 arises from the tergite of the same segment (Fig. 4b; d in Fig. 3E) and 31 from the endosternite of the foregoing segment (q in Fig. 3E; omitted in Fig. 4b). Both muscles insert on the coxal apodeme (Ca in Fig. 4b) and pull the coxa with the whole subcoxal complex in the anterior direction. (Forceful subcoxal pulling muscles would be inadequate because the segments are telescoped to some degree. Accordingly, muscles 82 and 71 are very slender - Figs 3 and 4b).

The articulations distal to the coxa are not suitable to lift the leg tip during the forward stroke and touch it down during the backstroke. Observations showed that this occurs by slight oscillating rotary movements of the coxa on its longitudinal axis (b-b' in Fig. lc). To avoid up and down movements of the median side of the coxae which would conflict with the need for flatness, one basal coxa articulation (III/cxv - in Figs lc,d, 2) has to be located near the median side of the coxa (Fig. 1d). A second opposed articulation (III/ cxd) permits the transmission of rotary movement of the sclerite II on axis a-a' to the coxa by the independently movable sclerite III (Fig. lc). The axes a-a' and b-b' are inclined to each other. If the coxa is not permitted to execute rotary movement on axis a-a' by muscles, it is forced to move on axis b-b' and sclerite III works like the movable connecting piece in a cardan shaft in which the axis of movement by articulations with one adjacent part is transverse to that with the other. Accordingly, the axis of movement between sclerite II and III (articulation II/III) is transverse to the axis of movement between sclerite III and coxa (articulations III/cxv and III/cxd). The subcoxal sclerites and their articulations are functionally important and this



Fig. 4. Metathoracic muscles of Lepisma saccharina, left side, integument shown as transparent, border of the muscle insertions punctured. Numbering of muscles according to Matsuda (1970). AC, antecosta. (a) Dorsal view with tergal longitudinal muscles, sites of dorso-ventral muscle insertions as in (b), outline of sclerite Id punctured; full circle, location of articulation Id/II; dashed line, ventral border of the paratergite. Anterior insertion of muscle 92 is on sclerite Id. (b) Lateral view with muscles of the leg base, coxoendosternal and trochantero-endosternal muscles not shown; a-a' and b-b' mark the planes of sections in Fig. 3E,F), respectively. Sclerotized leg parts marginally punctured; Id, Iv, II, III, sclerites of subcoxal segments; CX, coxa; Ca, coxal apodeme (dashed line). Muscle insertions: pt on paratergite, cx on coxa, en on endosternite; troch abd, abductores trochanteri. Muscles 83-86 said to connect the tergite with sclerite II were not found, the corresponding tergal insertions were observed to belong to muscle 61. Muscle 31 not drawn, it connects the coxal apodeme Ca with the endosternite of the preceding segment; together with 61 it protracts the leg base

seems to be the reason for the less-reduced condition of the subcoxal leg segments in Lepismatidae.

During the propulsive backstroke the whole leg complex is moved backwardly by contraction of both the very forceful muscle 25 (f in Fig. 3E,F) and muscle 92 (Fig. 4a,b). Simultaneously, the trochanter swings backwards by the contraction of muscles 50, 53–55 and 52 (Figs 2,3 and 4b), and the lateral margin of the coxa is pressed down by the contraction of muscles 25 and 53–55. Muscles 25 and 53–55 pull the posterodorsal margin of sclerite Iv (and indirectly the anterior margin of II) inwards and thus cause the slight rotary movement on axis a-a' (f and g in Fig. 3F). Contraction of muscles 74 and 63 raise the lateral coxa margin during the forward stroke. This skeleto-muscular arrangement allowed the formation of a sternal integumental fold which covers and mechanically protects the ventral side of the leg basis (s in Fig. 3A).

In Archaeognatha, the structures corresponding to the articulations III/cxv and III/cxd are on the lateral dorsal margin of the vertically arranged coxa, III/cxd being behind III/cxv (see Manton 1972: Fig. 31). It is probable that, starting from such an arrangement, the coxae were tilted backwardly by shifting the anterior articulation III/cxv in antero-ventral position. This would mean that this location of III/cxv is a synapomorphy of Lepismatidae (or even Lepismatoidea?) and Pterygota (compare Figs 4b and 10).

Judging from Fig. 52 in Boudreaux (1979), *Tricholepidion* exhibits all subcoxal sclerites but seems to be less stringently adapted to flat spaces. The coxa is more vertical and articulation II/III is close to articulation III/cxd, a feature indicating that the movement system is somewhat different from that in Lepismatidae. *Tricholepidion* is found in comparatively weak material like leaf litter or under bark, not under stones as are the Lepismatidae (Wygodzinsky 1961).

Autotomy and regeneration of legs

Other solutions to the problem of lifting and setting down the foot tips by utilizing more distal leg joints would be hard to envisage: the dicondylous coxo-trochanter joint with its now nearly vertical rotary axis is fully engaged in forward and backstroke, the trochantero-femur joint is specialized for autotomy and the more distal leg segments are acting nearly in the same plane (Fig. 1). Autotomy was observed when a leg of a Lepisma or Ctenolepisma specimen was prevented from rapid movement, e.g. by holding on the distal part with forceps. The proximal end of the femur is somewhat telescoped into the trochanter and fits tightly into it, like a stopper within a bottle-neck (Fig. 3D). Numerous small retractor muscle fibres hold the femur in position, and only when external force is large enough to overcome the muscular tension does the femur work itself loose and break off. Legs lost to autotomy in Ctenolepisma regenerated readily and appeared with the next moult after 6-8 weeks. The regenerated legs were fully functional, in colour slightly paler but otherwise similar to the previous ones. Other lost parts (scales, parts of antennae and caudal filaments) regenerate fully on the same occasions.

Fleetness

Lepismatidae are extremely fleet – when disturbed they run away very fast and stop immediately on finding a suitable retreat. The stride length is somewhat more than half the body length and the pace duration is, according to Manton (1972), 'of the order of 0.02 s or less'. Hence, the maximal frequency of leg movement is 50 Hz or somewhat more. The present observations on *Lepisma* and *Ctenolepisma* are in accordance with this statement. By measuring the footprints on a smoky glass plate, the stride length was found to be 6 mm for a *Lepisma* specimen of 11 mm body length and 8 mm for a *Ctenolepisma* of 13 mm body length. The corresponding running speeds were roughly estimated by comparison with reference speeds and found to be at least 0.3 and 0.4 m/s, respectively.

If a glass plate is held perpendicularly in the path of a fast running lepismatid, the animal does not bump into it with its head but turns aside and continues running along the plate. Assuming that the reaction is caused by contact with the antennae which are held in a V-shape in front of the head, the reaction time is of the order of 20 or 30 ms. The reactions are fast enough for correction movements even during free fall.

Posture during falling

If a lepismatid is dropped in any orientation from any height (even from few cm), it lands safely on the ventral side and is able to run away without time delay. The posture during the free fall was photographically documented by using a stroboscope with nearly 200 flashes per second against a dark background. The photographs show that during free fall the legs are stretched out latero-ventrally as far as possible and that the caudal filaments and antennae are spread as shown in Fig. 5. It seems that the spread appendages improve parachuting, reduce velocity and thus minimize the risk of injurious landing. At the beginning, the abdomen is curved dorsally causing the animals to turn until the ventral side faces the ground (Fig. 5a,b). This happens because the point of gravity is sufficiently distant from the point of drag. Thereafter the abdomen is held straight (Fig. 5c). No gliding was observed it seems that gliding is prevented by drag of the extended legs and diverging antennae. However, as shown by experiments with models, gliding should occur when the antennae and the flattened legs are pressed back against the body.

It is of interest for the discussion below that spiders dropped in any orientation likewise always land on the feet and quickly get away. As documented by photographs made with stroboscope, spiders somewhat raise their distal leg parts during falling; they thus raise the point of drag above the point of gravity and turn until the ventral side is facing the ground.

Experiments with models

As lepismatids do not utilize gliding themselves the principal gliding abilities of insects of lepismatid organization were studied on models imitating the lepismatid body in shape, size and mass. Legs were omitted in the models, imitating a posture with the flattened legs closely applied to the body and thus forming an aerodynamically effective ventral plane. The models were dropped from height H and the glide distance X was measured on the ground (Fig. 6). As in the falling experiments with living lepismatids, the models landed safely on the ventral side when the 'caudal filaments' were spread laterally and the 'abdomen' was curved dorsally as in Fig. 6a,b. Additionally, in this posture, the ventral plane of the 'thorax' is inclined optimally for gliding.

The complicated aerodynamic equations which are used in discussing physics of gliding (Kingsolver and Koehl 1985, 1994; Ellington 1991; Wootton and Ellington 1991) can be replaced, for the present purpose, by a very simple equation in which forces and velocities are eliminated. It is derived from the basic aerodynamic equations, valid for Reynolds numbers larger than one, and is more convenient for the exploitation of gliding experiments because it describes explicitly the glide distance X as a function of certain relevant features of the gliding object and of a non-linear function of height [f(H)]from which the object is dropped (equation in Fig. 6). The relevant features of the object are: the mass M, the horizontal planform area A, and a factor of proportionality which can be regarded as the gliding efficiency F of the object. The efficiency F and the function f(H) are a priori unknown, however, the product $F \times f(H)$ can be estimated from experimental data by using the equation in Fig. 6. For experiments with the same height H, the values of the products are measures of the



Fig. 5. Posture during falling, drawings after photographs made with stroboscope at 194 flashes per second. (a) *Lepisma saccharina*, drawings at intervals of 5 ms, middle drawing is 14 cm below the point of drop. (b,c) *Ctenolepisma* sp., distance below the point of drop: 16 cm (b), 30 cm (c)

relative gliding efficiencies of the objects, and for experiments with the same object and different heights H the products, as well as the glide distances themselves, permit impression of the function f(H) – for effects of different heights see Fig. 8.

The influence of the ratio A/M was tested by experiments with isometric flat models of different sizes, similar to lepismatids in outline and mass (Fig. 6). The measured glide distances exhibited considerable variance, mainly depending on whether the glide path was more or less straight within a vertical plane or curved with stochastic turns. Nevertheless, except for the smallest model I, the results shown in Table 1 (see p. 66) are in good accord with the equation. With increasing body size the distance X decreases drastically because the mass increases with the cube and the area only with the square of a linear measure. The violence of the impact on ground increased considerably with the size of the models.

The glide distance of the small model I is much reduced. It appears that, in contrast to the larger models, the inertial mass of this model is too small to stabilize gliding. The turbulent air stream relative to the falling object pulls the object out of its gliding attitude again and again, it staggers and goes more or less directly down. To determine the starting point of this effect, the weight of models of the optimal size II was altered by several steps and tested as before (Fig. 7). In the range of 8–16 mg, the mean glide distance follows the equation – the reduction begins immediately below 8 mg mass. The results mean that the gliding abilities are optimal for lepismatid insects of approximately 8 mm body length and 8 mg mass – and this is just the size of adult *Lepisma*. Larger and smaller insects should achieve smaller glide distances. The further experiments were therefore made with size II models.

It was supposed that increased glide distance might be attained by enlarging the 'thoracic' area around the point of gravity. Unexpectedly, the addition of slender 'lateral wings' (of the same form and size as in models IIB and IIC in Fig. 8) did not improve the gliding abilities if they were added to model II with dorsally bent abdomen and spread 'caudal filaments'. The glide distance was equal or even smaller than for model II without 'wings'. The extensions improved parachuting instead of gliding, indicated by slower descent. These undesired effects could be avoided by changing the 'posture' of the model II to model IIA with a nearly straight abdomen and the 'caudal filaments' put together to an unpaired projection (Fig. 8; IIA.b). The model IIA glided only when it was dropped in the gliding orientation as shown in Fig. 8b, but the glide path was nearly always in a vertical plane, in contrast to the often curved glide path of model II. If only the less curved events were taken into account for model II, the mean glide distances were the same as for model IIA (compare the X-values for II and IIA in Fig. 8).

Unlike model II, the addition of wings to the type IIA model significantly increased the glide distance as is evident from Fig. 8. The Mann-Whitney U-test showed that all X-values of models IIB, IIC, IID are different from the corresponding values of model IIA to the 0.001 probability level. The experiments with models IIB, IIC and IID showed that enlarging the wings increases the glide distance in particular if the wings are at least as broad as long. The X-values of model IID are significantly larger than the corresponding values of model IIC and IIB. Elongation of narrow wings as in model IIB does not improve the glide distance: for H = 1.0 m the distance for model IIB is even smaller than for model IIC (according to the Mann-Whitney test this difference is significant to the 0.01 probability level). This indicates that initially the wings had to be short and broad and that long slender wings are adaptations in the context of active flight. It should be noted that the addition of wings improved the attitude stability if they were somewhat raised as shown in Fig. 8c; the models glided if dropped in any orientation.

The product $F \times f(H)$ for the same heights H is a relative measure of the gliding efficiency F. The estimates of $F \times f(H)$ for the models in Fig. 8 and height H = 1.0 m were (in g/m) 160 for II and IIA, 93 for IIC, 58 for IIB, and 54 for IID. Remarkably, the wingless model of lepismatid shape has the greatest gliding efficiency! It is apparent that F depends on the breadth B of the models (i.e. the distance between their most lateral points in the region of the 'thorax'). Elongation of the anterior edge raises drag and reduces velocity, and the glide distance is reduced because it is proportional to the square of the velocity. This drag effect of small slender wings was already observed by Kingsolver and Koehl (1985) by their measurements on models in a wind tunnel. Increased glide distance is therefore only possible if, by adding wings, the quotient A/M is large enough to over-compensate for the reduced gliding efficiency. This is especially true when the added wings are nearly as broad as they are long or even broader.

This hypothesis was tested by experiments with a type IIB model stuck with plastic foam and equipped with 8 mm long and 3 mm broad wings which were stepwise shortened by cutting away parts of the tip (Table 2, see p. 67). The somewhat greater mass of the model improved its gliding performance: it glided perfectly straight. The glide distances measured were in accordance with the above hypothesis. They increased with the wing length until the wings were as long as



Fig. 6. (a,b) 'Lepismatid' models used for glide experiments. (a) Horizontal outline, L, 'body' length. (b) Side view in glide attitude, f, plastic foam stuck to some of the flat models, m, piece of metal. (c) Graph of the path of an object dropped from height H to the ground with horizontal travel X (= glide distance) due to aerodynamic effects; the equation describes the glide distance as function of features of the gliding object and of a non-linear function of height f(H)



Fig. 7. Mean glide distances X of flat models type II ($L = 8 \text{ mm}, A = 12 \text{ mm}^2$) with different mass achieved by sticking metal pieces of appropriate weight to the underside (m in Fig. 6b). Experiments as explained in Table 1 (H = 1.9 m). The curve is calculated from the equation in Fig. 6 for the constant $F \times A \times f(H) = 312 \text{ (mg } \times \text{ cm})$

they were broad, and decreased when the wings became longer. As expected, the estimated relative gliding efficiencies $F \times f(H)$ show, in rough approximation, linear regression in regard to breadth *B*.

Discussion of the evolutionary pathway

Pre-adaptations and scenario

The dicondylous mandibles of Lepismatoidea and Pterygota permitted the exploitation of wide range of food material

formerly not accessible to insects. It might therefore well be that the presumed lepismatid-like early ancestors of Pterygota were able to feed on living standing vascular plants. The basal parts of the stems were probably not suitable for this. [Lesions in fossil axes of *Rhynia* plants (Lower Devonian) are of a sort as made by arthropods with piercing mouthparts (Kevan et al. 1975).] More probably, the ancestors of Pterygota were to climb the plants and gnaw at the soft tissue of the shoot tips. Feeding in this way demanded leaving the already exploited shoots and climbing neighbouring ones. Every alteration which facilitated this change was of selective value until the optimal solution of the problem was achieved, namely active flight from one plant tip to another.

One of the first achievements seems to be the ability to recognize plant stems in the environment. Since the eyes of Pterygota are generally well developed, it must be assumed that the early pterygotan ancestor was diurnal and probably evolved the ability to search actively for suitable plants by walking in the direction of visually perceived vertical structures. That such an ability is within the scope of insect organization is shown by the analogous ability of the carabid beetle Calosoma sycophanta Linnaeus, 1758, which enters shrubs and trees in search for lepidopterous larvae and pupae. When walking on the ground the beetles are able to locate shrubs, and they have been observed to run in straight lines to them from a distance of half a dozen metres or so. Occasionally, it may happen that a Calosoma runs to and climbs a human person standing motionless in the landscape (observation made by the author). In contrast to the pterygotan line, the extant Lepismatoidea are active only in the dark and the eyes are more or less reduced - certainly a secondary situation.

Another possible improvement was leaving exploited shoots by dropping as a mode of fast, energetically inexpensive vertical descent. This was especially advantageous, when the shoot was densely covered with upwardly directed spine-like protrusions which hindered the descent, and/or when the phytophagous animals were attacked by carnivorous arthro-



Fig. 8. Glide distances X of the basic type II model (L = 8 mm, $A = 12 \text{ mm}^2$, M = 8 mg) and its modifications (IIA-IID). The models were dropped from different heights H in the optimal glide attitude (a for model II, b for the others); c = front view of the 'winged' models IIB-IID. Each value is the mean of 20 straight or nearly straight glidings by the same model. Vertical lines above the points indicate the standard deviation. Arrows pointing down indicate the reduced glide distance by model II when stuck with plastic foam (dashed line in a)

pods. If the attack was by spiders or arthropods with spiderlike habitus, the predators had a chance to continue the hunt on the ground by dropping when the prey had suddenly disappeared from the plant tip, provided the height of the plants was not too large (i.e. smaller than 1 m). Both the hunted and the hunter are able to land on their feet and to run away immediately (see section 'posture during falling'). Under these conditions selection favoured, in the phytophagous insect, the gliding ability which increased the distance between its landing point and that of the predator. Spiders were unable to glide, they have in contrast to lepismatids no pre-adaptations for this. For the hunted animal, even small gliding effects were advantageous because the survival chance is proportional to the square of the distance between both points – the average time the predator needs for its search is proportional to this area. In this scenario, parachuting effects are disadvantageous for the hunted animal because the drag lowers the glide distance and causes time delay which reduces the lead over the hunter.

That such a race was principally possible is shown by present day relations, e.g. between lepidopterous larvae and Ichneumonidae. Many larvae of Lepidoptera drop from their food plants when disturbed or attacked by enemies. On occasion, the author has observed an ichneumonid attacking a geometrid larva: the larva immediately fell down, the ichneumonid rushed in pursuit and found the larva by running search loops on the ground.

Extant lepismatids do not utilize gliding. However, they are pre-adapted for gliding in the following respects. (1) The dorsoventrally depressed body with laterally extended thoracic paratergites and backwardly directed flat legs form an aerodynamically effective plane on the ventral body side, enabling the initiation of gliding which can be improved by selection. (2) The very short reaction time enables the animals to adopt varying suitable postures during falling. (3) During falling, the caudal filaments (cerci and the terimalfilum or paracercus) permit the animals to turn themselves so that the ventral side faces the ground and is in an optimal orientation for gliding. As pointed out by Mägdefrau (1968), Smart and Hughes (1972), and Kevan et al. (1975), terrestrial vascular plants appeared in the Upper Silurian and were well developed in the Lower Devonian. Initially they exceeded not more than a few decimetres in height and reached 1 m height at the end of Lower Devonian. During this period the plants were of suitable size for the supposed evolutionary processes. Some of the plant shoots were densely covered with upwardly directed spine-like protrusions. In the further course of the Devonian the plants evolved to trees.

The fossil record shows clearly that carnivorous arthropods existed at the time in question, suggesting that the typical lepismatid adaptive zone was already realized. A very diversified fauna of fossil spiders is known from the Carboniferous, and arthropods of spider habitus had already appeared in the Lower Devonian (Petrunkevitch 1955; Kevan et al. 1975). Even today insects are the main prey of spiders and it may well be that this relation has been maintained since the origin of Pterygota.

Considering the optimal gliding size (8 mm body length) it seems that a glide distance at least in the order of 20 cm is sufficient to escape hunting enemies. This distance can be attained from heights of 1 m or more (Fig. 8). Selection for improving the gliding ability therefore occurred only when the height was smaller. Thus, improved gliding was in principle possible almost from the very beginning of the appearance of vascular plants. Shortening the way on ground or even landing on the next stem by improved gliding ability was advantageous. Once initiated, gliding was therefore further optimized by selection.

Presumed adaptations for gliding

The falling experiments with models showed that there is a 'window' for gliding in insects of lepismatid shape with the optimal size of approximately 8 mm body length and 8 mg mass. Insects with smaller than the critical mass are excluded from gliding (in contrast to active flight, which is possible for extremely small insects). Thus, the smaller juvenile instars were not able to participate in gliding and remained bottomdwellers. The lepismatid glide window has remained undetected because the former attempts to reconstruct the selective factors initiating insect wing evolution started from stick-like models (Flower 1964), much larger models with wings (Wootton and Ellington 1991) or were confined to measurements on larger models in wind tunnel (Kingsolver and Koehl 1985; for review see Ellington 1991; Kingsolver and Koehl 1994). However, Flower (1964) had already concluded from such experiments that, in accordance with the present findings, insects of approximately 1 cm length had the highest chance of evolving wings.

Gliding is improved when the mass is reduced as far as possible in the range above the critical mass and the thoracic paratergites are enlarged so that the lateral extensions are at least as broad as long. Utilization of this effect demands changes in posture during falling. At first, the abdomen must be curved dorsally and the tail bristles spread laterally to achieve gliding attitude. Thereafter the abdomen must be straight and the tail bristles put together. The falling experiments with living lepismatids and the extremely short reaction times observed show that such abilities are within the scope of lepismatid organization. Furthermore, it seems probable that gliding could be utilized to shorten the way on the ground to the next recognized plant by evolving the ability to control the glide direction by appropriate movements of the abdomen. (Walking to visually perceived plant stalks was important for effective exploitation of plants – see scenario.) Further optimizations concerns the improvement of landing (perhaps by reducing the velocity by spreading the tail bristles?).

The inevitable increase of the thoracic breadth in the course of gliding optimization has the disadvantage that the lateral extensions interfere with vertical environmental structures when the animals were running on the ground. Within the assumed scenario, selection thus promoted increased gliding ability through enlarged thoracic paratergites on the one hand and favoured unimpeded running over the ground on the other. The problem could be solved by turning the paratergites upwards when running and turning them horizontally when gliding. Because the zone between the paratergites and the leg base is membranous in lepismatoid insects, this effect could easily be attained via a strip of weakness within the tergite between the area of the insertions of the dorso-ventral muscles and the point above the articulation Id/II (Figs 3E.F, 4a and 9). [That this is possible in principle is shown by analogy in oribatid mites which evolved movable paratergal plates (Woodring 1962)]. The successive contractions of the dorsoventral muscles during running then pulled the median part of the tergite ventrally, pressed the lateral tergal parts against the subcoxal articulations Id/II, which now acted as pivots, and forced the paratergites into a vertical posture (Fig. 9). On the other hand, when the animal was falling, the dorsal longitudinal muscles were contracted and bent the terga so that the paratergites were forced into a more horizontal posture that was apt for gliding. This event explains the existence of the indirect flight muscles in Pterygota and why some of the dorsoventral muscles are bimodal, i.e. engaged in both wing and leg movement. The thoracic paratergal movements must have been simultaneous. It may well be that the somewhat disturbing paratergal muscles (1, 2, 3 and 92 in Fig. 4a) were reduced before this evolutionary step as a result of body mass reduction.

Once in place, the initially somewhat crude mechanism was optimized. The zone of tergal weakness was transformed into a hinge with a straight narrow strip of flexible cuticle. This hinge separates the parts of the wing from the tergal differentiations which evolved later, and is well seen as a straight structure in Paleozoic fossils (e.g. h in Kukalová-Peck 1978: Fig. 45). The leg base movements in the antero-posterior direction had to be abandoned by reducing the muscle 92 (Fig. 4a.b) and by in some way fixing the sclerite Iv to the anterior margin of the tergite as well as to the sternite. This initiated the evolution of the rigid thoracic box. The other leg movements had to be maintained together with the ability to appress the still flattened legs to the body during gliding. That part of Iv bearing the insertions of muscles 25 and 53-55 must therefore have been separated from the remainder by arthrodial membrane. The separated sclerite later became the basalare (BA - Fig. 10); this conclusion is supported by the probable homology of the trochanteral muscles 53-55 and p-tr2 (compare Figs 4a and 10). The pivot point of the paratergite (articulation Id/II) was now fixed and became the pleural wing process (WP - Fig. 10). The invaginated sclerite Id was automatically moved together with the paratergite and became in some way integrated into the wing (Fig. 9). Especially the sole pterale on the underside of the wing (pterale 2) seem to be



uns

tergite

Fig. 9. Schematic section illustrating movability of paratergite and sclerite Id after the hypothetical intercalation of the unsclerotized zone uns. The pre-existing articulation Id/II is the pivot for these movements. Id, II – subcoxal sclerites

a derivative of Id. This hypothesis is a modified version of Rasnitsyn's notion (Rasnitsyn 1981) that the wings are composites of tergal and pleural parts. Furthermore, it explains the ontogenetical relations between leg base and wings put forward by Kukalová-Peck (1983) and recent studies of gene expressions (Averof and Cohen 1997). As far as these arguments are conclusive they support the notion that sclerite Id is really derived from a former leg segment. [For criticism of the conclusions of Averof and Cohen (1997) see Wägele 2000: p. 151.]

Further possible optimizations were: (1) the uncoupling of the wing movements from leg movements by appropriate neuronal reorganization; (2) progress in reducing weight by evolving membranous parts and stiffening nervature on the basis of pre-existing blood lacunae within the wings; (3) beginning of further differentiations of the wing articulations by which the transduction of the tergal bending to the wing movements was improved. This included improved bending features in the tergum and the reduction of now unnecessary longitudinal tergal muscles. Finally, only 5 (=t14) and 6 (= t12) were retained as main flight muscles.

It seems inevitable that during the evolutionary phase of gliding, all thoracic segments were engaged in a similar way, and that not only the paratergites of the pterothorax but also those of the prothorax were movable. It is therefore not surprising that signs of prothoracic paratergite movability were found in Paleozoic Pterygota (see Kukalová-Peck 1978).

Presumed adaptations for active flight

With the above optimizations for gliding, a pre-adaptive plateau was attained from which active flight was accessible. The possible selection by predators was not eliminated by the optimizations because, for low falling heights, gliding was not sufficient to bring the animal out of the danger zone. Initiation of active flight was therefore of selective advantage. Active flight from one plant tip to another was so advantageous that its evolution went on even after the threat by predators ceased. Evolution was therefore proceeding without interruption towards active flight and, since there was no adaptive zone in which an intermediate stage of this process was optimal, no intermediate stage had the chance to be preserved.

The wings used for active flight evolved into elongated, more slender extensions and were restricted to the pterothorax; the

prothoracic appendages became immovable. This immobilization was probably due to the fact that the prothorax is too far away from the point of gravity and that the moments exerted by prothoracic wings would be too large. Furthermore, vibration caused by movable prothoracic wings are thus kept away from the head with its sensory organs.

Initiation of active flight was possible by neuroethological variation: flapping the wings up and down during gliding was apt to increase the glide distance. Adaptation for light weight favoured the development of somewhat passively flexible wing planes with more rigid leading anterior margins. During the down-stroke the wing thus became automatically pronated and during the up-stroke supinated generating components of lift and drive. Additionally, pronation could be supported by the contraction of the basalar muscles and supination by the muscles of the later evolved subalare.

During active flight, the legs no longer had to be flattened and appressed to the body and the subcoxal sclerites II and III could now be integrated into the thoracic box improving the mechanical stability of the flight apparatus. The dorsoventrally depressed body became more stick-like. Since the lepismatid muscular system of the leg base was, as it appears, at least partly transformed into the pterygotan musculature (compare Figs 4 and 10), the original spatial arrangement of the subcoxal parts had to be maintained. The axis of the basal articulations of the coxa remained unchanged (its ventral articulation is normally still in the antero-ventral instead of ventral position – Fig. 10) and the distal parts of the legs were vertically erected by appropriate torsion within the coxa.

Except for the pterygotan basalare, subalare and trochantinus, the lepismatid sternal and pleural membranous parts became sclerotized throughout, thus forming the rigid framework for the flight apparatus. Sclerites II and III were fused together and the part between the articulations Id/II and III/ cxd was stiffened by the pleural ridge (PL in Fig. 10).

As already stated in the previous section, that part of sclerite Iv which bears the anterior insertions of the muscles 53–55 and 25 had to be separated from the remainder by flexible cuticle and became the basalare (compare Figs 4 and 10). This is because the main part of Iv was integrated firmly into the rigid segmental framework whereas the ability of the subcoxal sclerites II and III to move was still important. With the reduction of the endosternite, the posterior insertion of muscle 25 shifted to the ventral part of the body wall near the anterior margin of the segment (p23 and p-s12 in Fig. 10). This was possible because the posteriorly directed movement of the leg base was no longer needed. Muscle 53–55 maintained its insertion on the trochanter abductor tendon, thus indicating the homology with the pterygotan p-tr2.

The basalar muscles are direct flight muscles and they are suitable for controlling the pronation of wings. Antagonistic supination of wings is possible by contraction of the subalar muscle t-cx8 (Fig. 10). In contrast to the basalar muscles its origin is not yet clear. One possibility among others is that the lespismatid precursor muscle of t-cx8 was engaged in the wing upstroke and located so far behind articulation Id/II that it caused supination at the same time. Candidates for this are the lepismatid posterior dorso-ventral muscles, probably muscle 63 (Fig. 4b). This hypothesis means that the effectivity of this muscle was improved by separating its dorsal insertion from the tergite on a sclerite of its own (the subalare) and shifting this sclerite firstly behind and then below the wing base.



Fig. 10. Typological scheme of pterygotan pterothorax, lateral view with lateral and dorsal muscles. Muscle names according to Matsuda (1970), names of the probably homologous lepismatid muscles (see Fig. 4a,b) below the pterygotan names. III/cxd, III/cxv – basal articulations of coxa; BA – basalare; CX – coxa; P3 – pterale 3; PH – phragma; PL – pleural ridge; SA – subalare; TN – trochantinus, WP – pleural wing process

The trochantinus appears as the anterior part of sclerite III which is either completely integrated into the thoracic box (as in all paleopterous insects) or separated by membrane from both the sclerite II and the caudal part of sclerite III (many Neoptera - TN in Fig. 10). Muscles t-til and t-til,2,3 which connect the tip of the trochantinus and the tergite tilt the axis going through both basal articulations of the coxa. This seems to be advantageous for crawling in the narrow spaces typical for the neopterous adaptive zone. In the paleopterous adaptive zone, this ability to move is useless and the trochantinus is integrated into the rigid thoracic box to increase stability. If the presented scenario is correct, the adults of early Pterygota were paleopterous and the movable trochantinus of the flying stage of Neoptera was secondary. However, contrary to the assumption of Boudreaux (1979), this does not necessarily mean that it is a completely new structure.

As pointed out in the ecological section, neoptery is probably due to the adaptation of the imago to nymphal food. Since in early evolution the nymphs were living in narrow habitats, the nymphs retained lepismatid characters within their locomotor system. For the ancestor of Neoptera, it was therefore easy to secondarily carry over the trochantinal ability to move from the nymph to the adult and to combine it with the imaginal thoracic box. That this was possible is shown by the fact that, in adult Plecoptera for example, the nymphal muscles are retained in the adult with few exceptions (Wittig 1955). Thus both views: that the separated trochantinus is a synapomorphy of adults in Neoptera and that it is homologous with the anterior part of sclerite III in Lepismatidae, are valid and do not exclude each other. The first approach exclusively compares the imaginal stages, the second one considers the complete organization, i.e. the holomorphe.

In the pterothorax, nymphs and adults of the neopterous Plecoptera exhibit trochantina which are similar to that drawn in Fig. 10. However, in the nymphal prothorax, the sclerite III (called coxopleurite) is separated from sclerite II (anapleurite) by flexible cuticle as in Lepismatidae (see Snodgrass 1935: Fig. 90). In particular the articulations corresponding to III/cxd, III/cxv and II/III are in the same positions as in Lepismatidae: the articulation II/III is far away from the articulation III/cxd (as shown in Fig. 1c) and not close to it as in *Tricholepidion*. It seems that the lepismatid pattern of subcoxal parts was maintained in nymphal Plecoptera because the nymphs lived permanently in habitats with narrow spaces. The still separated prothoracic sclerites III and II support the

view that the pterygotan pleuron really evolved by fusing subcoxal sclerites.

Summing up, it seems that the evolution of flight, once initiated with improvement of gliding, was canalized until active flight was achieved. The present synthesis supports the classical hypothesis that the evolution of wings started with gliding via paratergites. It presents a solution to the problem of how the paratergites became movable by utilizing lepismatid pre-adaptations. Furthermore, it supports the idea of Hinton (1963) that there were biotic factors (vascular plants, predators) which were responsible for selection which caused the corresponding transformations.

Evidence for the presumed transformations

The following facts can be taken as special evidence of the transformation from lepismatid to pterygotan organization. (1) A considerable part of the lepismatid muscle system seems to be homologous with muscles of Pterygota (see Matsuda 1970 and Fig. 10). In particular the existence of the pterygotan muscle p-tr2 which connects the basalare with the trochantinus supports strongly the transformation in question. (2) Comparative studies of motoneurone patterns supplying dorsal longitudinal muscles revealed a common pattern in Lepisma and Pterygota which is quite different from that in Chilopoda (Heckmann and Kutch 1995). (3) The two-bundled appearance of muscle t-p5,6 is explained by its origin from two different muscles: muscle 87/88 of subcoxa I and 81 of subcoxa II (compare Figs 4b and 10). (4) The antero-ventral articulation of the coxa (III/cxv) is in the same position in Lepismatidae and Pterygota (compare Figs 1c and 10). (5) The movable trochantinus of Neoptera is undoubtedly the homologue of the anterior part of sclerite III in Lepismatidae, moved by homologous muscles (compare Figs 4b and 10). (6) The separated subcoxal sclerites II and III in the prothorax of larvae of Plecoptera indicate that the pterygotan pleura are really derived from lepismatid subcoxal parts.

Ontogenetic aspects

Experiments have shown that insects with a mass smaller than 8 mg (and smaller than about 8 mm body length) were not able to glide. Thus, the smaller juvenile instars of the pterygotan ancestors were excluded from using the lateral extensions for gliding and had to remain substrate-dwellers. The diverging adaptive zones of non-gliding juvenile instars and adult instars capable of gliding necessitated differential adaptations: adaptations for different food, a need for extreme light-weight construction in adults which is of less importance to juvenile stages, etc. The problem could be solved by utilizing an 'ontogenetic switch' which enabled the independent accumulation of juvenile (nymphal/larval) and adult (imaginal) adaptations by a phase of organismic reorganization, i.e. metamorphosis. This switch is achieved in Pterygota by a reduced concentration of juvenile hormone during ecdysis. The amount of ontogenetic reorganization can be very different, beginning with very slight alterations (as in nearly 'ametabolous' post-embryonal development). However, the ground organization for both is generally built up during embryonal development.

The lepismatoid insects are ametabolous and this means that, at the beginning of the evolution of Pterygota, the adaptations for the adults could be only attained via morphogenetic alterations during embryonal development. It is therefore to be expected that the extensions used for gliding by early Pterygota must already have been present in the youngest instars, formed as if they were functional. However, for the juvenile stages living on the ground such extensions were disadvantageous, as they were in the adults when running on the ground. Improvement was possible by the same adaptations as in adults: by the ability to move the lateral extensions up and down. Finally, however, the most successful solution for the juvenile wings was to reduce the size of the lateral lobes, apply them to the body backwards and immobilize them by fusion with the tergite. This final stage is generally found in extant non-endopterygotan insects.

These considerations are in accordance with the fossil record presented by Kukalová-Peck (1978). She found that in Paleozoic nymphs the wings were laterally directed thoracic outgrowth with signs of actual or former ability to move, i.e. more or less pronounced hinge structures with pteralia, even – as residuals – on the prothorax. In Paleozoic nymphs of Ephemeroptera and Megasecoptera, the wings were large lateral outgrowths considerably exceeding the lateral border of the trunk, but streamlined by being curved backwards (see Kukalová-Peck 1978: Figs 28 and 31). Possibly, such extensions were engaged in secondary roles. In other lines, the outgrowths did not or did only little exceed the lateral border of the trunk, nevertheless they still exhibited signs of former ability to move (Kukalová-Peck 1978: Figs 22, 24, 33 and 35).

Nymphs with movable wings must have existed for many million years and there arises the question why juvenile instars did not likewise achieve active flight which is physically possible even for very small individuals? The ultimate reason for this is probably the same as for the other animals which evolved the ability to fly. Juvenile Chiroptera begin flying shortly before they attain the terminal size, however, they cannot fly perfectly until they are fully adult (Kleiman and Davis 1979; Corbet and Harris 1991). In Aves the situation is similar. This suggests that body growth and active flight cannot be successfully combined, perhaps because active flight demands extremely sophisticated organization, which cannot be achieved when the tissues are growing. There seems to exist a 'rule of incompatibility of growth and flight'. Thus it can be taken for granted that, from the very beginning, active flight was exclusively achieved by adult individuals of the ultimate size, i.e. imagines. In early Pterygota, the ability to moult in the imaginal stage was still present as is indicated by the subimaginal moult in Ephemeroptera. The fact that all other extant Pterygota do not moult in the imaginal stage is probably a result of selection for light weight. Moulting demands fully functional epidermis cells even within the wings. As pointed out by Maiorana (1979), degeneration of the epidermis in wings is a means of improving the wing efficiency with the result that, except for Ephemeroptera, functional wings are confined to only one instar: the last and reproductive stage. Further she pointed out that the subimaginal moult in Ephemeroptera was apparently retained because it is needed to complete the elongation of caudal filaments and forelegs of adults. These elongations are special features of the reproductive system of mayflies and cannot develop during nymphal life. Accordingly, the subimagines exhibit very low flight activity: they fly only from the water surface where they emerge to the bank or shore and start to moult to the definitive imago.

The avoidance of mechanical interference with the environment caused the exopterygotan nymphs to develop their external wing anlagen to backward-directed, immobilized small extensions. Endopterygota attained a still further step. Starting from exopterygote nymphs, the anlagen became invaginated and disappeared completely as external appendages. This endopterygoty made possible extremely varied annidation of the larvae, resulting in the unusually high number of extant species. As pointed out by Hinton (1948) it is apparently not possible to realize the transition from an endopterygote stage to functioning wings during one moult. It was therefore inevitable to retain an exopterygote juvenile stage at the end of larval life. Since this stage fitted neither in the imaginal nor in the larval adaptive zone, it evolved to the quiescent pupa. That the pupa should be regarded as a nymphal rather than as a subimaginal stage is shown by the fact that, in larvae of Lepidoptera for example, the pattern of tactile setae is maintained nearly unchanged in the pupa, whereas the imago develops a completely different new set of tactile setae (Hasenfuss 1997). Tactile setae which are experimentally heat damaged in a larva, are missing in subsequent larval instars and the pupa. In the corresponding imago, however, the patterns of sensilla develop undisturbed (Hasenfuss, unpublished experiments).

Ecological aspects

The present hypothesis assumes that the preflight ancestors of Pterygota had biting mouth parts and fed initially in all instars on weak tissue at the tips of vascular plants (meristem, stages of fructification) reaching new plant stems by running on the ground. This implies a terrestrial mode of life on comparatively dry uplands in all stages. The evolution of gliding and active flight in the adults gave rise to diverging adaptive zones for these and the juvenile instars (nymphs, larvae). The imagines were fluttering from plant tip to plant tip still feeding on weak tissue, their adaptive zone was doubtless that of paleopterous insects, i.e. the wings could not be folded on the back. The wing movements were primarily synchronous as is still observed in extant Ephemeroptera ('eosynchronous flight' - Brodsky 1994). The juvenile instars remained substratedwellers and had to eat other food, probably dead, decaying plant material.

Continued damage of the plant tips caused the plants to evolve protective devices reducing the amount of food accessible to the flying insects. The substrate-dwelling nymphs were not affected by this. The problem could be solved via the following strategies. (1) No food uptake by the imagines; this strategy is followed by the extant Ephemeroptera, for example. The males ingest air in the gut, thus forming stiff support for the long abdomen - a very effective method to reduce weight as an adaptation in the context of the nuptial dancing flight. (2) Becoming carnivorous as in Odonata. (3) Breaking through the plant barriers mechanically by modifying the mouthparts for piercing and sucking. This is a very successful strategy which possibly evolved several times independently. It is met in the haustellate Paleozoic insects including the paleopterous Palaeodictyoptera, Megasecoptera and Permothemistida as well as the neopterous Diaphanopterodea (see, e.g. the reconstruction of diaphanopteroid haustellum by Kukalová-Peck 1985). Most Paraneoptera are likewise equipped with piercing mouthparts. (4) Exploiting the same food as the flightless juveniles.

A disadvantage of the original bipartite adaptive zone is the fact that colonizing new habitats is only possible if both the

juvenile and the imaginal stages find appropriate conditions, especially suitable food. Both strategies (3) and (4) are appropriate to master this difficulty. The development of hard piercing mouthparts enabled the animals to exploit a great variety of living plant material which cannot be managed using biting mouth parts. Equipped with the same piercing mouthparts, nymphs and imagines may nevertheless have quite different life styles as is shown by Cicadidae for example, with soil living nymphs and aerial imagines. In this context it is of interest that the nymphs of Palaeodictyoptera and Megasecoptera possessed haustella, as did the adults, and that they were probably terrestrial (Smart and Hughes 1972). The onisciform shape of palaeodictyopteran nymphs (see Wootton 1972) fits well in this scenario.

Strategy (4) was very successful and led supposedly to neoptery, i.e. the ability to fold the wings on the back. Except for Plecoptera and Endopterygota, strategy (4) is found in nearly all extant Neoptera, and even within Endopterygota it was attained by the largest group – the Coleoptera – which protect the folded hind wings by heavily sclerotized elytrae. The utilization of the same food material by both juveniles and adults was therefore of great selective advantage. Neoptery permitted the imagines to crawl to the same sites as the juveniles without being impeded by the protruding wings.

Thus there are two adaptive zones in regard to wing posture: that of neoptery in which the imagines are able to crawl within narrow spaces on the ground and in vegetation, and that of paleoptery in which the imagines are unable to do this. That the inability to fold the wings can be advantageous is shown by butterflies and skippers (Papilionoidea, Hesperoidea) within the otherwise neopterous Lepidoptera: they secondarily lost the ability to fold the wings by secondary adaptation to the adaptive zone of paleopterous insects. From this, the question arises as to whether the paleopterous Ephemeroptera and Odonata are primarily so or were secondarily derived from neopterous ancestors.

Recent Ephemeroptera and Odonata seem to be primarily paleopterous. From the outgroup criterion follows that if the Metapterygota (Odonata + Neoptera) are really monophyletic, then the paleoptery of Ephemeroptera and Odonata is most probably plesiomorphic in regard to Neoptera. This hypothesis is supported by differences in adhesive devices which are important for hold on smooth plant surfaces. In Ephemeroptera, the adhesive pads are zones of flexible cuticle ventrally at the base of the pretarsal claws, and in Odonata adhesive devices are missing (Beutel and Gorb 2001). However, in extant Neoptera the typical adhesive devices are the very effective unpaired arolia between the pretarsal claws. Judging from Fig. 33A in Kukalová-Peck (1985), even the extinct neopterous Diaphanopterodea seem to have possessed arolia. It is likely that arolia evolved in the context of neoptery and that this happened only once. It is unlikely that Ephemeroptera and Odonata evolved from a stage with arolia because in those Lepidoptera which are secondarily incapable of folding their wings (Papilionoidea, Hesperiidae), the arolia are still present. These conclusions support the notion that Diaphanopterodea are cladistically true Neoptera and that their haustellum evolved independently from that of paleopterous hastellate taxa. According to Rasnitsyn (1981) there are no significant differences between Diaphanopterodea and Neoptera in wing articulation structure.

The swamp woods of the Carboniferous and early Permian offered rich possibilities for diversification and annidation in insects. Typically, many bottom dwelling forms or stadia were forced to adapt to unpredictable changes of water level and became thus amphibious or even aquatic. This offers an explanation as to why the supposedly primary paleopterous Ephemeroptera and Odonata acquired aquatic nymphs – a certainly secondary mode of life. The mode of respiration is very different in the nymphs of both taxa indicating independent adaptation to aquatic life. Small appendages on legs and other body parts described and figured by Kukalová-Peck (1987) for many Paleozoic insects possibly functioned as gills. Gill vestiges may even be retained in aerial stadia as shown by some extant Plecoptera.

It is improbable that the aquatic life style of the nymphs of Plecoptera is due to adaptation to swamp wood conditions. The plecopteran nymphs are generally rheobiontic and are the only Pterygota which retain the lepismatid condition in which subcoxae II and III are distinct sclerites in the prothorax (Snodgrass 1935). This suggests that the nymphs became aquatic at an early stage of neopteran evolution and that they were thereafter permanently living in running water, adapted for life either within the thin zone at the surface of the submerged stones in which the flow velocity is low or within the gaps between the stones. This life in narrow spaces is probably the reason for the maintenance of the mentioned lepismatid feature.

Preservation of ancient features

The above discussion confirms the view that ancient characteristics had especially good chances of being maintained in evolutionary lines which otherwise became very specialized. If, at an early level of organization, such characteristics were integrated within specialized constructions, they were saved from further alterations and could survive even hundreds of million years. Thus the specialized lepismatid type of locomotion within flat spaces favoured the preservation of thoracic leg base structures which enabled the identification of three subcoxal leg segments. In Ephemeroptera, ancient characteristics (such as the subimaginal moult, the synchronous wing movements, the retention of three caudal filaments, etc.) could only be preserved because they became an integral part of an elaborate mating system with the nuptial dancing flight of males. In Plecoptera, as noted above, ancient characters of the locomotory system were maintained, as it seems, because their nymphs were adapted for life in running water at an early stage of neopteran evolution.

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Zusammenfassung

Ein möglicher, von der lepismatiden Organisation ausgehender Evolütionsweg zum Flugvermögen der Insekten

Ausgehend von der Hypothese daß die Evolution des Flugvermögens der Pterygota mit der lepismatiden Organisation ihrer Ahnen begann, wurde die funktionelle Anatomie des Thorax von *Lepisma saccharina* und einer *Ctenolepisma* sp. im Hinblick auf Adaptationen an die adaptive Zone der Lepismatidae und im Hinblick auf Praeadaptationen für die Evolution der Pterygota untersucht. Es wurden in der Pleuralzone gut erhaltene Teile von drei subcoxalen Beingliedern

gefunden, die an der Beinbewegung teilnehmen. Die Strategie der Lepismatidae, vor Feinden durch rasches Laufen zu fliehen und sich in flachen Spalten zu verstecken, führte zu einer dorsoventralen Abflachung des Körpers, die beim Herabfallen Gleiteffekte und weitere Flucht am Boden ermöglichte. Im Zusammenhang mit der vermuteten Ernährung von Triebspitzen der im Devon noch niedrigen Gefäßpflanzen eröffnete dies einen kanalisierten Evolutionsweg zum aktiven Flug wobei möglicherweise spinnenartige Prädatoren den Selektionsdruck verstärkten. Gleitversuche mit 'lepismatiden' Modellen zeigten ein enges Gleitfenster mit dem Optimum von 8 mg Gewicht und 8 mm Körperlänge. Es wurde eine Gleichung gefunden, die die Gleitdistanz als Funktion der Gleitfläche, der Masse, der Gleiteffizienz des Fallkörpers und einer nicht-linearen Funktion der Fallhöhe beschreibt. Vergrößerung der Gleitdistanz war möglich, wenn die Körpermasse veringert, die lateral vorragenden thorakalen Paratergite vergrößert wurden und als 'Flügel' nicht länger als breit waren. Die Behinderung der Flucht am Boden durch laterale 'Flügel' konnte durch deren Vertikalstellung beim Laufen und durch Horizontalstellung beim Gleiten vermindert werden. Die Beweglichkeit war durch Einfügen eines Membranstreifens zwischen Tergit und Paratergit sowie die Nutzung des vorhandenen Gelenks zwischen zwei basalen Subcoxalgliedern mit dem vorhandenen Muskelsystem möglich. Demnach ist der dorsale Teil eines ursprünglichen Beingliedes im Flügel der Pterygota integriert. Auf- und Abbewegung der Flügel während des Gleitens ermöglichten den Beginn des aktiven Fluges. Die dafür erforderlichen Transformationen sowie deren ontogenetische und ökologische Aspekte werden diskutiert.

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