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CONTRIBUTIONS OF FUNCTIONAL MORPHOLOGY TO THE PHYLOGENETIC SYSTEMATICS OF ODONATA

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The comparative functional morphology of the flight apparatus, the male secondary copulatory apparatus and the female ovipositor of Odonata are described. The investigations lead to a reconstruction of the evolution of the different mechanisms and contribute to the phylogenetic systematics of Odonata. — 1 — Although the flight apparatus of the three main groups of Pterygota (Odonata, Ephemeroptera, Neoptera) show fundamentally different features, inspection of the functional morphology has revealed that the differences are not unbridgeable. This comparison established new homologies and resulted in the reconstruction of an ancient flight apparatus of Pterygota ("Ur-Flugapparat"). The extant types of flight apparatus of Odonata, Ephemeroptera and Neoptera — provided with highly autapomorphous characters — can be derived from the "Ur-Flugapparat" in three functionally different lines of evolution, which are mutually exclusive. It may be concluded that flight ability has evolved only once, supporting the hypothesis of a monophyletic origin of the Pterygota. Although the problem of phylogenetic relationships between the three subgroups of Pterygota remains unsolved, there are indications that Ephemeroptera and Odonata are sister groups. — 2 — In the "Ur-Flugapparat" the dorsolongitudinal muscles presumably were used to produce an arching of the tergum during the downstroke ("tergal arching mechanism of flight"). This ancient function of dorsolongitudinal muscles has been modified fundamentally in the Odonata. Abandoning the use of meso- and metathoracic dorsolongitudinals as power stroke-muscles, the unique indirect-direct flight machinery of Odonata was developed — powerful (but nearly independent) — in both flight segments. — 3 — The evolutionary developments of the flight apparatus within the Odonata have mainly concerned the mechanisms of wingstroke-plane alteration of the fore- and hindwings, leading to two different main types of fliers : "precision-manoeuvre fliers" (Zygoptera, Anisozygoptera) and "forward-thrust fliers" (Anisoptera). — 4 — Dragonflies use three non-homologous parts of the male secondary copulatory apparatus as a functional "penis" : the ligula (in Zygoptera), the hamuli posteriores (in Anisozygoptera) and the vesica spermalis (in Anisoptera). The zygopteroid mode of sperm-transfer via the ligula is thought of as the primary mode. An attempt has been made to reconstruct a continuous transformation series between this type and the different types of Anisozygoptera and Anisoptera, and to evaluate phylogenetic implications. Comparative analyses of the male vesica spermalis and the female ovipositor result in further hypotheses concerning the phylogenetic relationships of the subgroups of Anisoptera.

THE PHYLOGENETIC POSITION OF THE ODONATA

Before discussing the phylogenetic relationships of different subgroups of Odonata, it is important to consider the phylogenetic position of the Odonata ***as a whole*** within the group Insecta. The clarification of this problem is of basic importance, because it is most essential to know the large-scale systematic position of the group to which a subgroup belongs, if one is to assess specific characters of the subgroup. However, the opinions and arguments about the important question of how to position the Odonata within the system of the Insecta are still subject of discussion today. Several different suggestions exist (see for instance HENNIG, 1969 ; KRISTENSEN, 1975) which are founded mainly on morphological characters. These characters seem to be rather isolated and "picked out at random". This means that up to now these characters have usually not been investigated sufficiently as functional parts of organs (mechanisms, synergs etc.), and this (besides real "specialization crossings" ; HENNIG, 1966) has led unavoidably to different estimations of their phylogenetic value. In Figure 1a-c the three phylogenetic trees are shown which assume a ***monophyly*** of the Pterygota, but disagree in the exact position of the three subgroups ; in Figure 1d the more unusual version of MATSUDA (1970, 1981) is illustrated, which negates the monophyly of the Pterygota and also for example the existence of a monophyletic group Dicondylia.

The reasons for my own view of the phylogenetic position of the Odonata within the Insecta stem from comparative research on functional morphology of the flight apparatus of Odonata and other Pterygota (PFAU, 1986 and former papers). In the following, only some details — those which are estimated as being the most essential for the phylogenetic positioning of Odonata — are presented. These are the results from functional morphological experiments on the wing- and wing-base mechanics of freshly killed animals, which are tested by working models (Fig. 3). Most of the results are in strong disagreement with former studies, mainly to the detailed study of TANNERT, 1958 (see PFAU, 1986 : tabelle 1 and p. 112-117). The paper of TANNERT is to a large extent responsible for the dissenting hypothesis of MATSUDA (Fig. 1d).

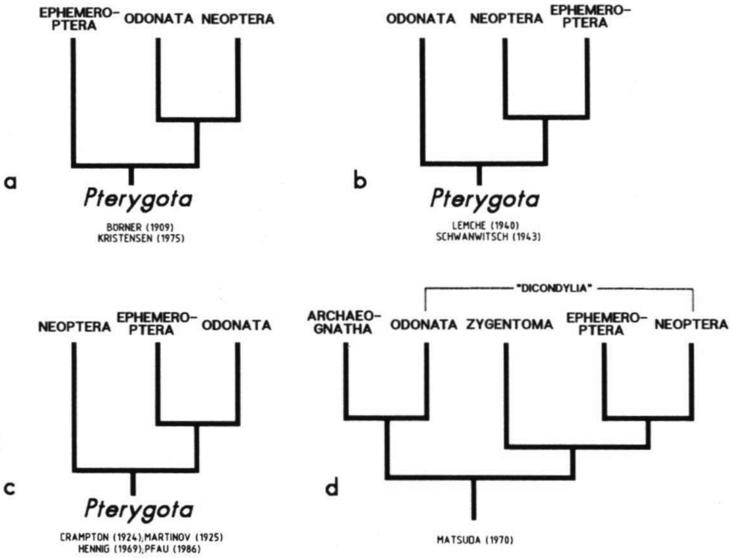

Fig. 1. Different phylogenetic trees of Pterygota: (a-c) for citations see Hennig, 1969; — (d) Matsuda's (1970, 1981) hypothesis, assuming non-monophyly of Pterygota, the dichotomic phylogenetic tree drawn according to his statements.

The base of the dragonfly wing is formed by two large sclerites, the costal plate (CP) and the radio-anal plate (RAP; Fig. 2 and 3. In Tannert's study these plates are designated as "Costalplatte" and "Radius-Analis-Platte"; the latter is shortened to "Radioanalplatte" in Hennig, 1969 and Pfau, 1986). These two plates are connected via hinges to the tergum and to the pleurum. Since the pleural ridge separates dorsally into *two* fulcra ("a" and "b" in Fig. 2-5), there exist *two* fulcrum-to-wing joints, one to the CP and one to the RAP: each plate articulates with its own fulcrum. The axis of the up and down stroke of the wing is a hinge-joint-axis, which is defined by the two fulcrum-to-wing joints (axis A/B; Fig. 2).

In Figure 2, in the two halves of a pterothoracic segment of a dragonfly the muscles are separated according to functions. On the left side mainly the direct downstroke (bas1, sub1) and indirect upstroke muscles (dvm1) of the wingstroke-motor system, which produce the wing down- and up-movements, are drawn (in addition three muscles for the stroke-"fine adjustment" are illustrated on this side — see later). In the middle and on the right side muscles are shown which cause changes in the angle of the plane of the wing stroke (dlm, pa) or in the angle of attack of the wing, that is the angle of pronation and supination (hca, fa; vca, sub2, sub3 — see different texture of muscles). The fact that several of these muscles are involved in different functions has

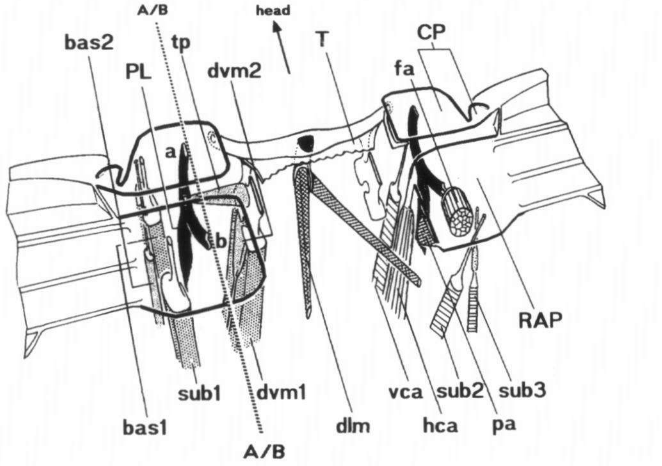

Fig. 2. One segment of the dragonfly pterothorax, seen obliquely from above; the tergum is almost totally left out. CP and RAP pronounced and drawn transparent. Left side shows the direct downstroke muscles (bas1, sub1), the indirect upstroke muscle (dvm) and the muscles of unilateral power-control and click-mechanism (bas2, dvm2, tp); mid and right side show stroke-plane muscles (dlm, pa), pronators (hca, fa) and supinators (vca, sub2, sub3). A/B: wing stroke axis defined by joints a and b.

not been incorporated in this figure ("polyfunktionelle Muskeln", see Pfau, 1986: tabelle 1 and p. 91-101).

During the downstroke, when the ***direct wing depressors***, the basalar and subalar muscles (bas1, sub1; Fig. 2, 3), contract, ***both*** basal plates of the wing, the CP and the RAP, are lowered together with the whole wing (Fig. 4b). On the other side of the fulcra, the tergum — which is ***not*** connected to the pleurum via cuticular bridges as usual (Snodgrass, 1935, fig. 96: prealare and postalare = "Tergalarm" and "Lateropostnotum" in Weber, 1933) — is lifted passively as a whole, just as if it would represent an undeformed plate ("Tergalplatten-Mechanismus" or shorter TPM, Pfau, 1986: p. 78 f.). In the Odonata there exists ***no*** arching-mechanism of the tergum for the downstroke as in the other Pterygota where it is brought about by contraction of the dorsolongitudinal muscles dlm (Fig. 7) — in this group the dlm's are specialized for new functions (see below). When the ***indirect dorsoventral muscles*** dvm1 (Fig. 2, 3), which were stretched during downstroke, contract, the wings are moved upwards (Fig. 4a). In addition there are tiny tonic dorsoventral, basalar and subalar muscles, which are (for instance) able to control the stroke power unilaterally (Fig. 4: dvm2, bas2, (sub3)) — and there also exists a (tonic) muscle which varies the strength of a click-mechanism of the tergum and pleurum, superimposed on both wingstroke phases (Fig. 2: tp; for further details see Pfau, 1986, p. 45 f.).

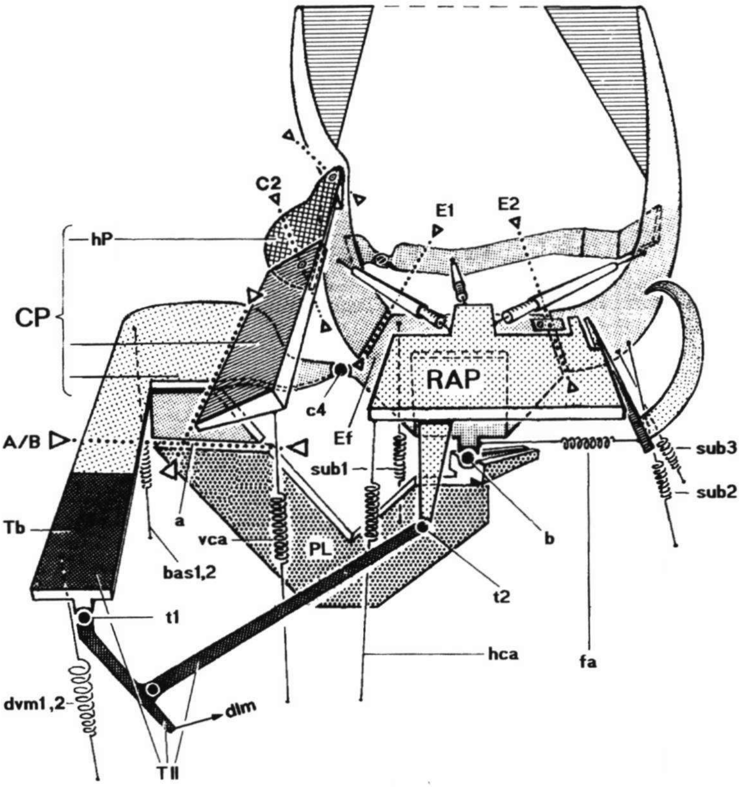

Fig. 3. Working model. The right forewing (including some tergal elements) is seen obliquely from above from the inside of the body. CP and RAP are strongly simplified. Only sclerites are represented ; since the soft membranes between CP and RAP are not present, the structures (sclerites, joints) of the ventral surface of the wing base are visible — for instance the joint "c4" or the lateral joints of the epifulcrum (here indicated only by axes : E1 and E2 ; see also Fig. 5a-d). Muscles are represented by tension springs ; ▷ indicate moving-axes.

Besides the wingstroke there are of course possibilities for further wing movements in the Odonata : — 1. The rotary or pronation-supination-movements of the wing which are mechanically rather complicated and occur in two mechanical different ranges of rotation, which are limited against one another by mechanical stops (Fig. 5a-b ; c-d — for further details see Pfau, 1986). — 2. There is a possibility of forward-backward movement. In the following only the forward-backward movements of the wings of dragonflies will be considered.

The mechanism of the mesothoracic forward movement of the wing is illustrated in Figure 6 (for the metathorax, see below). The RAP of the

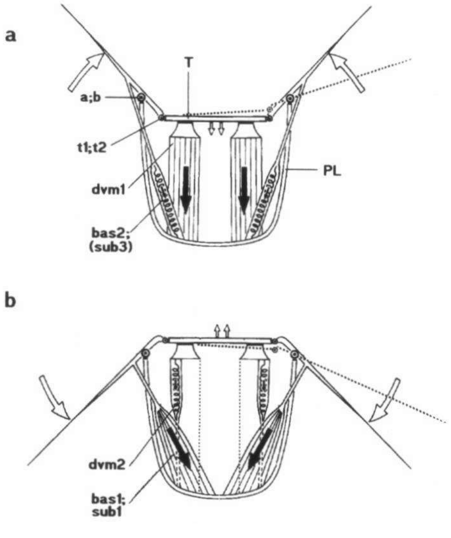

Fig. 4. Upstroke (a) and downstroke (b) : dvm2, bas2 : "tension-spring like" power-control muscles of downstroke resp. upstroke (see Pfau, 1986, p. 45). — Muscles bas1 and sub1 are left out in (a), muscles dvm1 are only indicated by dotted lines in (b). Dotted wing- (and tergum-)profiles indicate asymmetric wingstrokes of reduced amplitude, brought about by stronger unilateral contraction of muscles bas2 resp. dvm2.

forewing can be moved around an axis, which is defined by two joints : one on the upper surface of the CP (c2) and one on the lower surface (c4 ; see also Fig. 3 and Fig. 5a — c4 is not shown in Fig. 6). This axis is therefore indicated here by C2/C4. During the forward-movement of the wing a frontal part of the mesotergum (Tb, "Tergalbrücke"), which is hinged onto the CP's of the left and right wing at the points t1, is rotated backwards (around axis T1/T1) when the dorso-longitudinal muscles (dlm) contract. The tergum, which lies caudally to the tergal bridge, is thereby moved backwards and upwards, and — via the lateral pivot point between the RAP and the tergum (t2) — the RAP is moved backwards around C2/C4. The result (simplified here) is a movement of the whole distal wing forwards. In this special movement the proximal costal plate CP* forms a solid reference plate with respect to the tergum, the RAP and the rest of the wing. (In contrast to this, during the wings up and down movement (Fig. 4) the CP and the RAP are moved in like manner, and during the rotary movements (Fig. 5a-d) different combinations of movable parts of the CP and RAP are used.)

The dlm's which swing the wings forwards therefore do not contribute noticeably to the power of the downstroke in the Odonata. As already mentioned, during the downstroke mainly the direct basalar and subalar

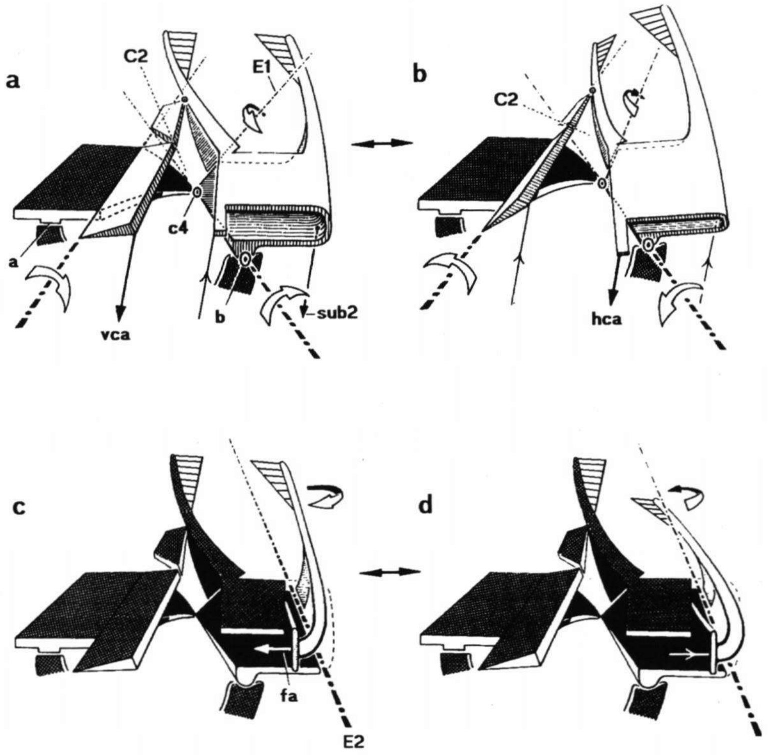

Fig. 5. Mechanics of wing rotary movements (pronation : a- > b and d- > c ; supination : b- > a and c- > d). Notice the different direction of axis C2 (= hinge joint axis running through joint c2) in b compared to a : the wing forward-movement (Fig. 6) is blocked in b since axis C2/C4 is not functional (see also Pfau, 1986, p. 57 f.). Parts which are not moved (representing the solid reference-parts for the moving parts) are marked black.

depressor-muscles cause the downstroke of the wing (Fig. 4) ; the tergum is lifted only passively (as a whole plate) via the lever arms of CP and RAP, as the wing moves downwards.

The mechanisms of the dlm's in Ephemeroptera (Fig. 10c), in Neoptera (Fig. 10d) and in a hypothetical ancestral flight apparatus (Fig. 10a), however, are very different. In these, the dlm's contribute essentially to the downstroke : the contraction of the dlm's bends the tergum, so that it forms an arch and this pushes the wings down (Fig. 7 ; "Tergalwölbungs-Mechanismus" or shorter TWM, Pfau, 1986 : Abb. 23 and p. 78 f.). The essential lever which transmits the forces to the wing in the Neoptera is the axillary 1 (ax1 ; Fig. 10d), whereas in the Ephemeroptera an axillary is used which lies more caudally ("ax4" ; Fig. 10c — possibly not homologous to the axillary 4 of

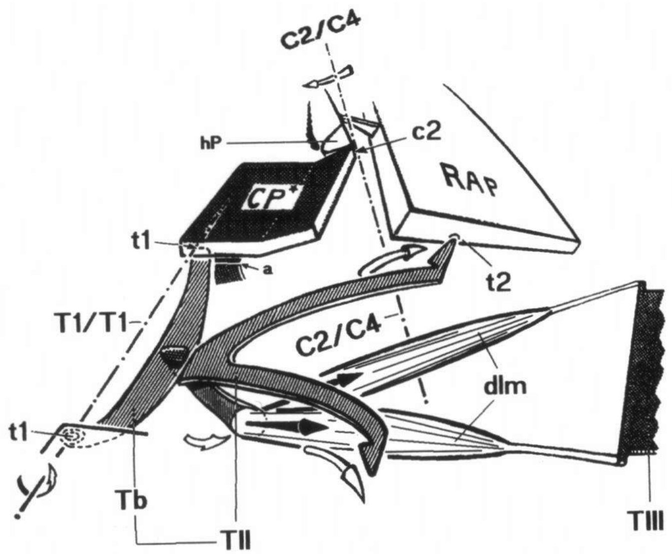

Fig. 6. Mechanism of forewing forward-movement. See text. Wing and tergum are seen obliquely from above. For the second joint of axis C2/C4 see Fig. 3, Fig. 5a or Fig. 10b.

Neoptera). During the downstroke of Neoptera and Ephemeroptera the indirect dlm's are assisted by the basalar and subalar direct downstroke muscles (Fig. 7b). These muscles lift the tergum indirectly as a whole (and bend it) — in addition to the (direct) tergum-bending by means of the dlm's.

Surprisingly even the basic mechanisms of the wingstroke of Insecta are incorrectly illustrated in most textbooks and popular books on insect flight (Fig. 8). The mechanisms of the other wing-movements (for instance the wing-rotary movements) up to now have been largely neglected. This curious fact demonstrates an aggravating deficit of scientific efforts, which for instance has led to several non-applicable opinions about the evolution of insect flight. Besides this the progress of physiological understanding of flight (i.e. interpretation of many physiological data) has been retarded (this even concerns physiologically "best-studied" sense organs of flight ; see for instance Pfau, 1983 and Pfau, *et al.*, 1989).

In Figure 9c the forward movement of the wing of Odonata by means of the dlm's is shown again (more schematized). However, this function of the dlm's applies only to the mesothorax and forewings (II in Fig. 9c), whereas the dlm's of the ***meta***thorax (III) in Zygoptera and Anisozygoptera move the wing ***caudally*** when they contract — using a different tergal mechanism (for this mechanism see Pfau, 1986 : p. 61 f.). These ***opposite*** functions of the dlm's in the two adjoining segments of the flight apparatus are the main reason for my postulation that formerly (in an ancestral flight apparatus ;

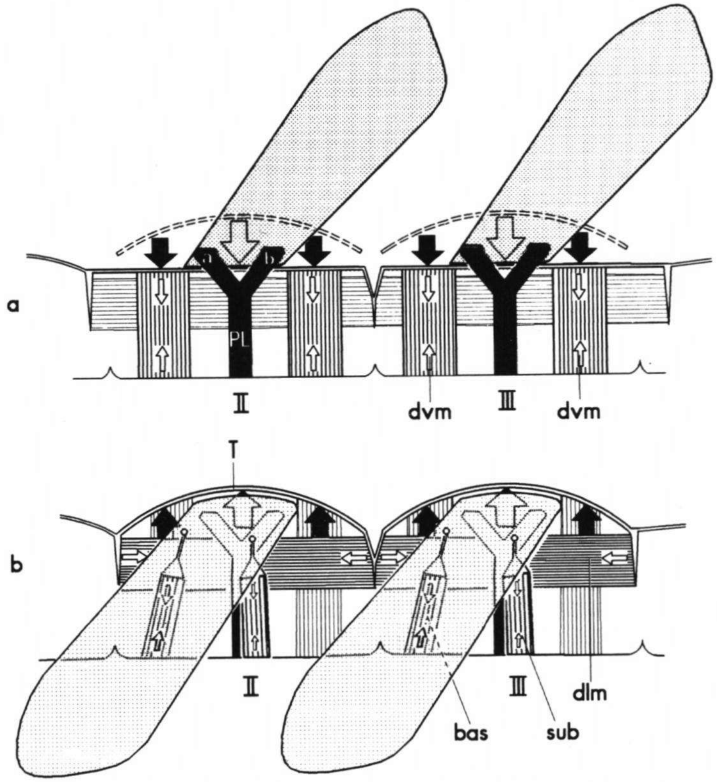

Fig. 7. "Tergal arching-mechanism" of flight : (a) Upstroke ; indirect muscles dvm only partially flatten the arching of the tergum — partially this movement is passively achieved by elastic forces : (b) Downstroke ; the indirect muscles dlm are assisted by the direct basalar and subalar muscles. — Only the pleural ridge (with its two fulcra showing the primitive state !) is illustrated ; further pleural structures, for instance those which support the tergum (prealare and postalare), are left out. II, III : meso-, metathorax.

Fig. 9a, 10a) the meso- and metathoracic dlm's both functioned as power downstroke-muscles [1], bending the tergum similarly in the meso- and metathoracic segment ("tergal arching-mechanism" or TWM ; Fig. 7). At this ancient stage the meso- and metathoracic dlm's would have to be activated synchronously in order to generate sufficiently strong downstrokes, and this means that the meso- and metathoracic flight segments formerly were dependent on each other.

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[1] This is in contradiction to the generally accepted opinion that Pterygota have started to fly with a "direct flight motor mechanism" — such as figured in Fig. 8a.

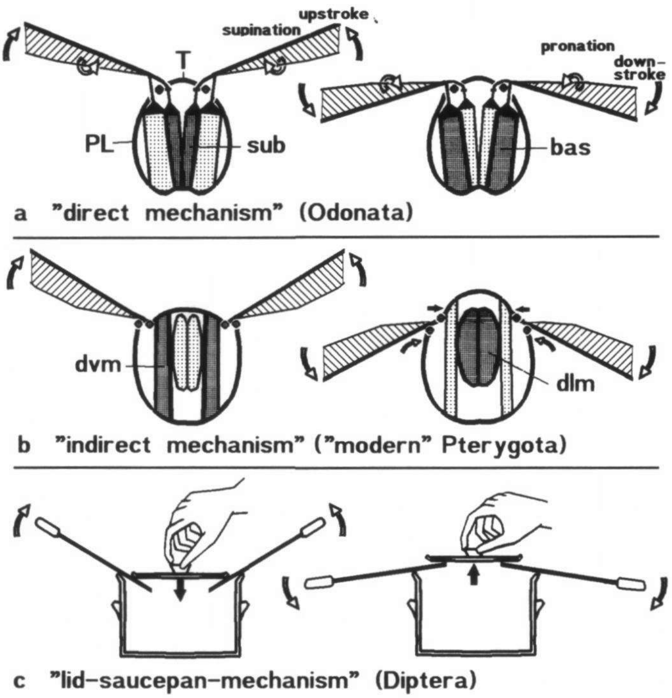

Fig. 8. Incorrect models of insect wingstroke (adapted from NACHTIGALL, 1968, figs 30-32): (a) Wingstroke-mechanism of Odonata — often (wrongly) labeled as the "primitive" mechanism in Pterygota. This schematic drawing, however, is also incorrect with respect to the antagonism of direct basalar and subalar muscles (as well during the up- and downstroke as during the wing rotary movements). In reality the stroke-mechanism of Odonata is a mixed indirect-direct mechanism (Figs 2, 4), whereas the wing rotary movements are "movements of their own", which are much more complicated (Fig. 5a-d). In contradiction to this picture the basalar-1-muscle can be considered as a mere depressor muscle, whereas the subalar-1-muscle is a *down*stroke muscle with an accessory supination-function. — (b) The mechanism of downstroke in Neoptera cannot be understood sufficiently by demonstrating thoracic cross sections. Moreover, in these cross sections the illustrated arching of the tergum is wrong (and otherwise cannot be managed by means of the dlm); this sort of tergal arching in a cross-section area would even counteract the downstroke. In contrast to this, Fig. 7 shows a lateral aspect of the flight segments, demonstrating the principal arching of the tergum in a longitudinal section area. — (c) The so-called "lid-saucepan mechanism" ("Deckel-Topf-Mechanismus") is a model which is only able to illustrate the up and down wing movements in principle as a result of a lever-mechanism. This model can be at best compared to the odonatan stroke mechanism (Fig. 4). In contrast to this the mechanism of Diptera is a most derived "TWM-mechanism", which in its fundamental details has been described correctly by BOETTIGER & FURSHPAN (1952); the model of PRINGLE (1957) has been built according to this study and is explained very intelligibly in ALEXANDER (1968, p. 52 ff.); for further models of dipteran wingstroke see also PFAU (1987) and in prep.

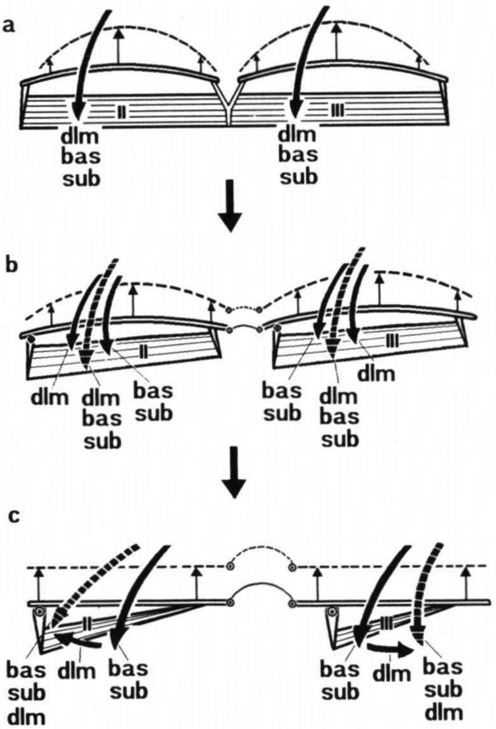

Fig. 9. Evolution of opposite dlm-functions and decoupling of meso- and metatergum. Dashed arrows indicate resultant wing trajectories (see text): (a) Hypothetic ancestral stage. For the mechanism of dlm in II and III (= TWM) see also Fig. 7. — (b) Hypothetic transition stage. — (c) Extant (primitive) stage of Zygoptera and Anisozygoptera. — The dlm-antagonist pa (see Fig. 2), which enlarges in both flight segments the scope of stroke-planes, is not illustrated. In the Odonata the tergum is lifted passively during the downstroke as a whole (see dashed tergum-line), caused by the action of direct basalar and subalar wing-depressors (see also Fig. 4); for the mechanism of dlm in II see Fig. 6. The wingstrokes of mesothoracic (II) and metathoracic wings (III) are shown as synchronous movements in this figure, but only in the Odonata (where the terga are decoupled — as a result of a functional modification of the dlm's) also very effective asynchronous wingstrokes of fore- and hindwings can be accomplished.

In order to derive the ***different*** functions of the dlm's in the meso- and metathorax of extant Odonata from the ancient stage, one has to assume that an intermediate stage existed (Fig. 9b) in which the dlm's on one hand still were indirect downstroke muscles, working via the arching-mechanism of the tergum, while on the other hand they had already achieved additional accessory functions — and these were different in the two segments, moving the wing frontally in the mesothorax and caudally in the metathorax. Besides supporting the basalar and subalar direct downstroke muscles, the contraction

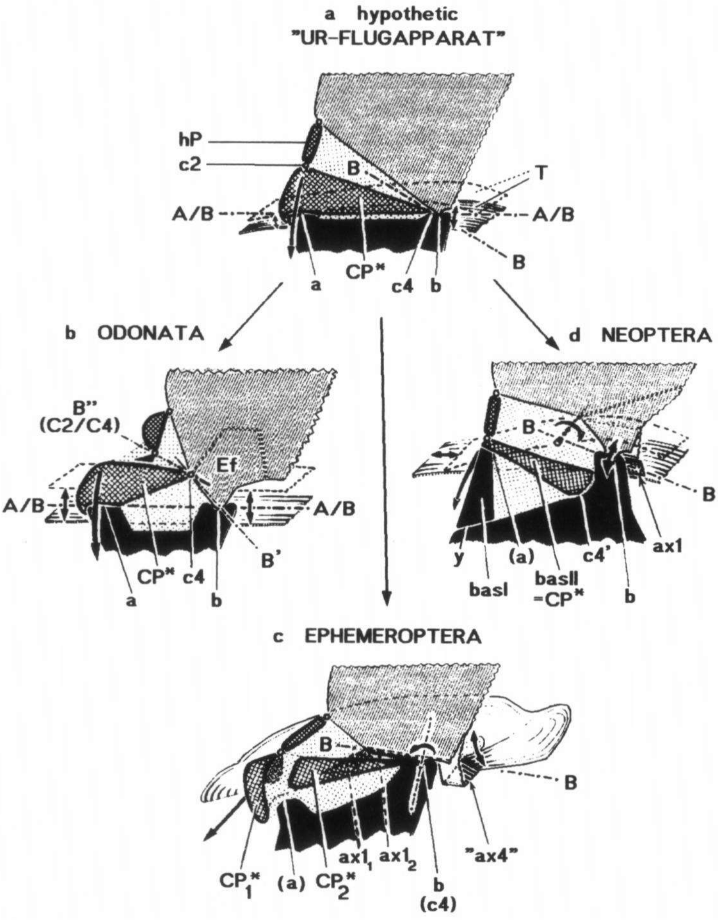

Fig. 10. Evolution of flight mechanisms in Pterygota. Homologies are expressed by texture: (a) "Ur-Flugapparat" : TPM + TWM ; — (b) Odonata : TPM ; — (c) Ephemeroptera : TWM1 ; — (d) Neoptera : TWM2. — (TWM resp. TPM — except in the Ephemeroptera — are indicated by dotted tergum-lines.) Left wings in the upstroke position seen from outside ; the distal wing is cut ; only a frontal and central section of the wing base is illustrated. Membranes are dotted widely. Some important axes of movement are indicated by –.–.– (to be compared also with Figs 2-6 for the Odonata). B is a second wing stroke axis (TWM-axis) which has been taken over from the "Ur-Flugapparat" in the Ephemeroptera and Neoptera. The Odonata are the only Pterygota which kept the stroke axis A/B ; axis B has been "modified" strongly in this group (- > B', B"). In the Ephemeroptera the CP is divided into CP^*_1 and CP^*_2 ; the frontal stroke-joint "a" in this course has lost its function. In the Neoptera the basalare I (bas I) is shown as a newly formed pleural sclerite — only a rest of the CP* is represented in the lower wing surface by the basalare II (bas II). The frontal stroke joint "a" again lost its former function (as a convergence to Ephemeroptera). For further explanations see Pfau (1986).

of the dlm's therefore simultaneously caused a change of the wing trajectory — in segment II to the front, in segment III to the back. Now the dlm-downstroke function via the arching mechanism of the tergum (originally the main function of the dlm's) only had to be reduced and the surprising opposite functions of homologous muscles in two adjoining segments of Odonata are achieved (Fig. 9c).

The meso- and metathoracic mechanisms of dlm's of the Odonata therefore are derivable from an ancient mechanism of Pterygota (Fig. 9a, 10a) and this "reconciles" a difference between Neoptera-Ephemeroptera and Odonata, which has been valued as fundamental, namely the use or not of dlm's as power downstroke muscles. This was one of the reasons why MATSUDA postulated a convergent evolution of the flight apparatus and flight ability in Odonata and Ephemeroptera + Neoptera (for other reasons of MATSUDA see comments of PFAU, 1986 : p. 105 f.).

In the extant Odonata the mechanisms of the meso- and metathoracic terga are not coupled functionally via the dlm any more (see above). Thus the dragonflies are the only insects today which can actuate the fore- ***and*** hindwings very effectively and almost independently, with any phase difference.

Different groups of the Neoptera (Coleoptera, Strepsiptera, Hymenoptera, Lepidoptera part., Diptera) and the Ephemeroptera have "by-passed" the deficiency of dlmII/III-interdependence in another way : in these groups one of the two flight segments has been more or less reduced and the wingstroke efficiency has therefore been improved only in the remaining segment. In all these cases the tergal mechanism of the (remaining) power flight segment has been modified drastically (for the Diptera see also legend to Fig. 8c).

Further evolutionary modifications of flight mechanics in Odonata — going beyond the ancient flight mechanisms of the Zygoptera-Anisozygoptera (Fig. 9c) — occurred in the Anisoptera. In this group the dlm's were almost completely reduced in the metathorax (note that the antagonistic pleuro-alary muscles (pa, Fig. 2) have been completely reduced in both flight segments of Anisoptera). On account of this loss of a degree of freedom, the metathoracic wingstroke motor system could be simplified. Since in addition a steeper plane of wing-movement was achieved in both segments by developing a more vertical alignment of the segments [2], the Anisoptera are specialized forward-thrust fliers par excellence, while retaining good hovering ability. In the Zygoptera and Anisozygoptera, on the other hand, the stroke plane angles have a larger variability — in ***both*** segments independently — and these groups can be labelled as "precision-manoeuvre fliers".

To clarify the question whether the Pterygota are monophyletic or not, and to determine the phylogenetic position of the Odonata, a comparison

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[2] In the metathorax this seemingly compensated for the loss of the dlm's ; the "loss of lift", which followed the reduction of muscle pa in this segment, presumably was equalized by the broadening of the hindwings.

was made between the odonatan wing mechanics (Fig. 10b; see also Fig. 4, 5a-d, 6) and the mechanics of Ephemeroptera (Fig. 10c) and Neoptera (Fig. 10d). The results are only summarized here (for further explanations see Pfau, 1986, p. 75-91).

An attempt to derive the different types of extant flight apparatus from one another — in all possible combinations — or from a hypothetical ancestral apparatus (Fig. 10a) was made while developing continuously the different possibilities of wing movement of each extant flight apparatus. However, it was not possible to derive (without constraint) for example the neopteran mechanism from the ephemeropteran one, or the odonatan one. Nor was it possible to derive the mechanism of the Odonata from that of the Neoptera or Ephemeroptera — and so on. Concerning their flight apparatus all three groups are strongly autapomorphic. On the other hand it was relatively easy to derive each type from a hypothetical ancestral flight apparatus. For such a hypothetical apparatus, at the base of the Pterygota, a combination of the tergal plate mechanism (TPM) and tergal arching mechanism (TWM) is assumed ("Ur-Flugapparat" — "TPM + TWM"), in which two wing stroke axes (A/B and B) are used. Only this combination of mechanisms for producing the wingstroke leaves open all the possiblities which were developed later, and it seems that an insect with such a mechanism already had quite good capabilities to fly.

Accordingly the three types of extant flight apparatus are considered as three functional alternatives evolved from a common ancestral flight mechanism. In contradiction to Matsuda who found principal differences (seemingly evaluated as unbridgeable) between the flight apparatus of the Ephemeroptera + Neoptera and of the Odonata, and therefore derived the Odonata and their flight ability totally separately (i.e. convergently) from the Apterygota, these results show that the Pterygota as a whole (including the Odonata) are very probably monophyletic and that the ability to fly evolved only once.

I would like to draw attention to the double wing hinge of the Odonata (Fig. 10b), which, according to this hypothesis, has been taken over from the "Ur-Flugapparat". The frontal fulcrum-joint "a" (and therefore also the axis A/B) has lost its function (independently) in the Ephemeroptera as well as in the Neoptera, but its position can still be reconstructed if homologies between sclerites, as shown here, are taken into account. Difficulties of deriving the neopteran basalaria (and the special function of basalare-muscles) from the ancient flight apparatus lead to the assumption, that the basalare I is a newly evolved structure in the Neoptera — originating within the pleuron by the development of a joint "y". In the Neoptera therefore only the basalare II has "survived" as the rest of the CP* in the lower surface of the wing. This assumption is explained (and supported) in Pfau, 1986 (p. 88 f.; joint "y" is indicated there as "f", the CP* as BAS).

The fact that in the Pterygota three functional alternative flight apparatuses exist has the consequence that the problem whether the Odonata are the nearest relatives of the Neoptera or of the Ephemeroptera cannot be solved by a comparison of flight mechanics at present. However, when looking at small sclerites in the dorsal region of the wing base and at the edge of the tergum of Odonata and Ephemeroptera (which are not shown here), one can state that there is a strong similarity of form, positional relationship and muscular equipment in these two groups. This indicates that the Odonata and Ephemeroptera are closely related, forming sister-groups (see Pfau, 1986 : p. 87 f.). Therefore the phylogenetic tree of Fig. 1c is probably the correct one. If this hypothesis can be supported, it would mean that the stem species of Odonata has to be reconstructed from an Odonata + Ephemeroptera stem-species (and not from an Archaeognatha + Odonata stem-species as implicated by Fig. 1d). This should be essential in future evaluations of characters.

THE PHYLOGENY OF SUBGROUPS OF ODONATA

The phylogenetic system of Fraser

This well-known phylogenetic system of the Odonata (Fraser, 1957) has been selected for discussion here on account of its completeness (the fossil taxa for instance are incorporated) and on account of several interesting new aspects. However, it is also an example of an almost purely morphological system : Fraser mainly compared the venation of the wings which seemed to have the advantage of sufficient complexity and, besides this, offered an opportunity to integrate the fossils.

Hennig (1969, preamble) however has shown very convincingly how uncertain the fossils are as evidence for phylogenetic systematics. On the other hand, the character-complex "wing venation" — represented relatively well by the fossil record — is rather problematic because it is difficult to evaluate the functional and adaptive value of its details, that is to assign venation characteristics to categories of functions and to evaluate for example the possibilities of convergent evolution. The stem-group region of the Odonata ("Odonata" in a broader sense) therefore has been left out here. Furthermore, there is nearly no fossil documentation of those structure-function complexes dealt with in this paper, but these in any case would have to be studied first in the extant groups.

Fraser's system (Fig. 11) is a typical one of the era before Hennig. Fraser did not distinguish clearly between common primitive features (symplesiomorphies), derived features (synapomorphies) and convergently evolved features. So his "annectent affinities" — often found between one group and several other different groups (sometimes obviously in contradiction to his own phylogenetic tree ; see below) — appear to be only morphological resemblances. Incongruent phylogenetic systems of that type (showing obvious inconsistencies between cladogram and classification) are often founded on mere symplesiomorphic resemblances which reflect simply anagenetic levels. They bear a strong resemblance to the so-called "evolutionary classification"

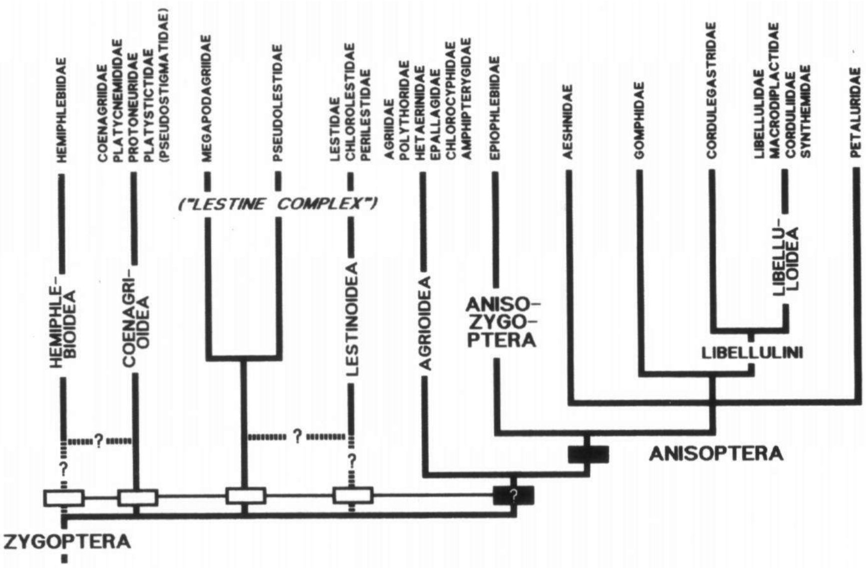

Fig. 11. Phylogenetic system of Odonata (Fraser, 1957) — a little modified (for instance all extant groups now reach the same horizontal level). "?" indicate vaguenesses between Fraser's text and his phylogenetic tree-figure.

(Mayr, 1974), which was qualified by Hennig (1974) as "a variant of aristotelian typological classifications".

Fraser seemingly did not intend the establishment of groups as monophyletic unities. Many groups in the future will presumably come out to be artificial, founded on account of symplesiomorphic correspondence. An example is the so-called "Lestine Complex" : Fraser found a relationship of this "group" to the Anisozygoptera (he thought that the Anisozygoptera would have arisen from the "Lestine Complex") ; otherwise he also postulated relationships of parts of the "group" to other taxa, considering for instance the Pseudolestidae as an "annectent" between the "Lestine Complex" and the Agrioidea, whereas the Megapodagriidae should form a link to the Coenagrioidea. If one tries to incorporate all these statements in a phylogenetic tree, it cannot be made congruent. Even the most interesting (possibly synapomorphic) wing-vein character of Agrioidea + Anisozygoptera + Anisoptera "$IR_3 + R_{4+5}$ recessed to proximal of nodus" may either be thought of as a multiple convergent feature (because it is also found in the Lestinoidea-group Lestidae and in the Pseudolestidae) or some of the groups may be suspected to be artificial.

One of the most essential results of Fraser is the hypothesis of non-monophyly of the Zygoptera — or (more precisely, in the sense of Hennig) the paraphyly of this group. This means a branching pattern, where single groups of Zygoptera branch from the stem, each of them forming the sister group with the rest of the Zygoptera, in each case including the Anisozygoptera

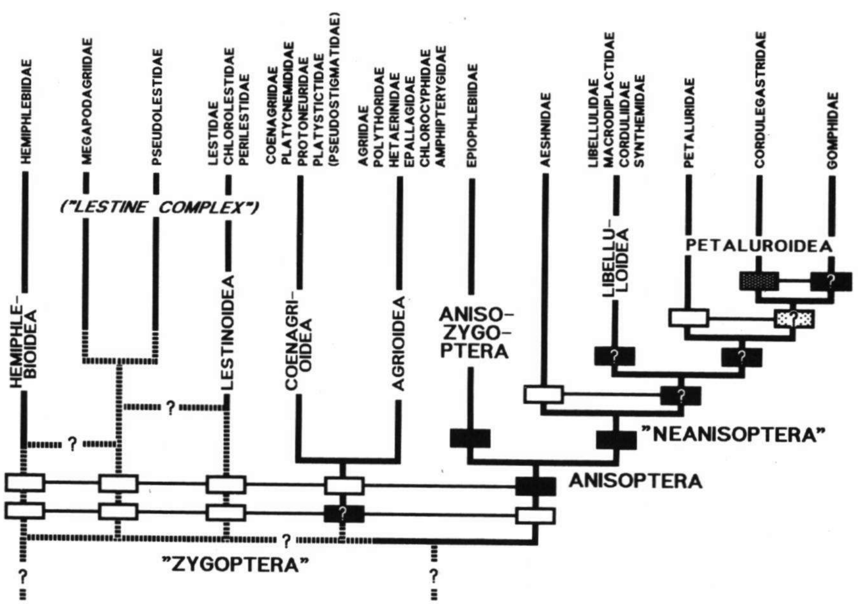

Fig. 12. Phylogenetic system of Odonata according to comparative functional-morphology research (Pfau, 1971, 1985, 1986). The possibility of monophyly of the Zygoptera is incorporated with a second (dotted) basic stem. For the question-marks in the synapomorphy-boxes see text.

and Anisoptera (Fig. 11). But this most essential result up to now seems not to be substantiated by convincing arguments (for possible monophyly of Zygoptera see below).

PHYLOGENETIC IMPLICATIONS FROM FUNCTIONAL MORPHOLOGY

My own (fragmentary) system of Odonata phylogeny (Fig. 12) is again based on comparative research in functional morphology. In this system some groups (and basic branchings) of the Zygoptera, proposed by Fraser, have been adopted as a "preliminary platform" — however only the branchings signed by the black boxes are suggested as possible monophyletic groups, substantiated by synapomorphies in the sense of Hennig.

In the Zygoptera only one synapomorphy-box is illustrated in Fig. 12. In several families of Zygoptera there exists a presumably synapomorphic character in the lateral region of the metathoracic tergum : a relatively big sclerite "vTS" ("vorderer Tergalsklerit"), which has been enlarged in correlation with a reduction of a sclerite "hTS" ("hinterer Tergalsklerit" ; see Pfau, 1986 : Abb. 1a and p. 109 f.). Since this apomorphic character is found in several groups of Coenagrioidea *and* Agrioidea (but possibly not in all subgroups, therefore the "?" in this synapomorphy-box), it may indicate quite a different phylogenetic branching of the Zygoptera as compared to FRASER's system (Fig. 11).

The secondary copulatory apparatus

Transformations of the ancient zygopteroid type and possible monophyletic origin of Zygoptera. — The male secondary copulatory apparatus of Odonata has evolved mainly from the sternal sclerites of abdominal segments II and III (Fig. 13). Again this is an apparatus which represents a unique "invention" peculiar to the Odonata, a true autapomorphy of this group. The belief, that it is very unlikely — in spite of the drastic morphological and functional differences between Zygoptera, Anisozygoptera and Anisoptera — that the

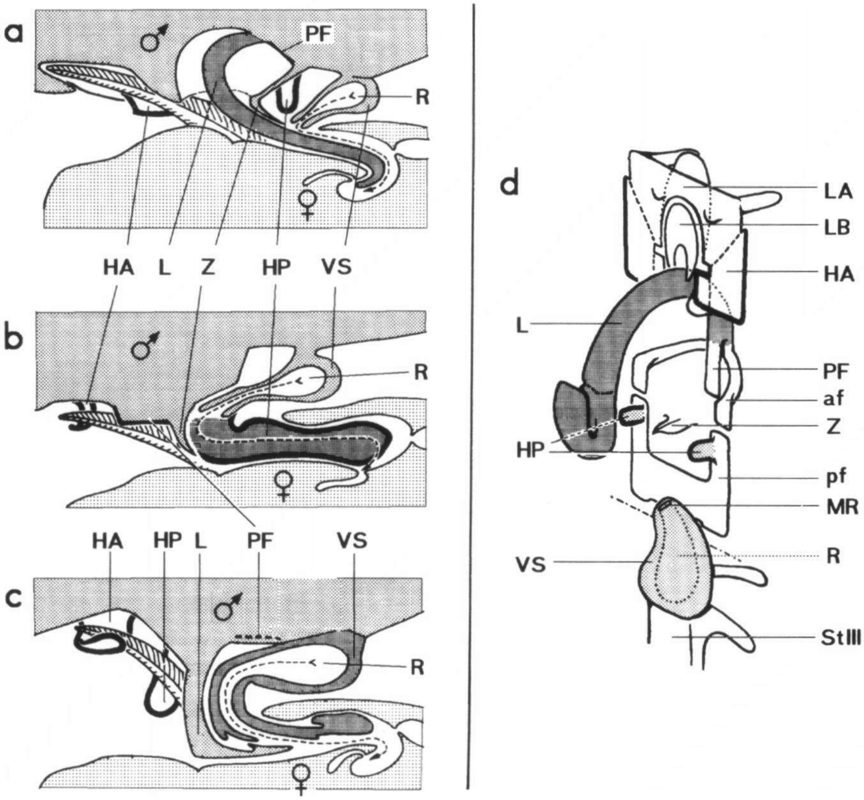

Fig. 13. Longitudinal sections through the different types of male secondary copulatory apparatus of Odonata during sperm-transfer (a-c). — Sternal sclerite-components of the apparatus of Zygoptera (d). The ligula, as the primitive "penis" is dotted densely, the other parts to differentiate to functional penes (HP : Anisozygoptera ; VS : Anisoptera) are dotted more widely. The segments are positioned upright.

secondary copulatory apparatus has been evolved convergently within the Odonata, consolidates the monophyletic origin of the Odonata *. (For the essential discrimination between stem groups and "*-groups" see HENNIG, 1969 : p. 32 ff. Many confusions and misunderstandings concerning the mono- or polyphyly of groups result from the fact, that no difference was made between these categories. In fact we are not able in most cases to place fossil "taxa" (forming the stem-group region of an extant group) exactly within a *-group, i.e. within a group which contains all descendents of the last common stem-species of all extant species.)

It is very astonishing that in dragonflies there are three different modes of sperm-transfer to the female (Fig. 13a-c). In these three modes three non-homologous structures of the male secondary copulatory apparatus (which in all extant groups is homologous as a whole without doubt — see above and later) function as a penis. In the Zygoptera (Fig. 13a, d) the sperm is conducted in a furrow (fu, Fig. 16a) of the ligula (L). In Anisozygoptera (that is the only extant genus *Epiophlebia*) the paired hamuli posteriores (HP; see also Fig. 14) are pressed against each other and act as a penis consisting

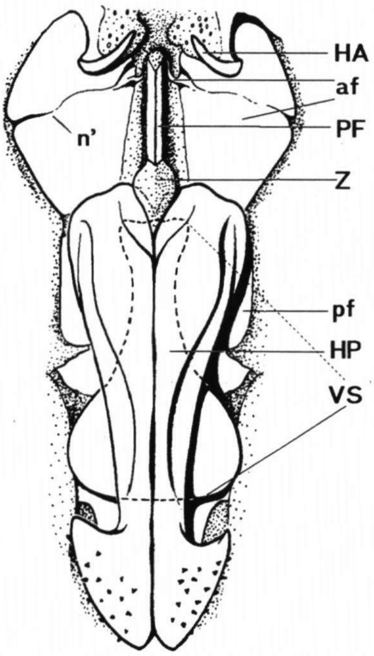

Fig. 14. Secondary copulatory apparatus of *Epiophlebia superstes*. — n': suture which indicates the former ("zygopteroid") extension of the base of the anterior frame (see also PFAU, 1971, p. 356).

of two halves which form a tube for sperm transfer (Fig. 13b). In Anisoptera it is the vesica spermalis (VS) of the third abdominal segment (the temporary sperm-reservoir in all three groups) which becomes the functional penis (Fig. 13c).

The sperm-transfer mode of the Zygoptera (Fig. 13a, d) is probably the primitive one. That is, it has preserved substantial primitive features, for instance a primitive vesica spermalis which is short and consists only of one segment, and a ligula which is used as a sperm-conduit. There are some reasons for this assumption. **First**, it seems very likely that the Anisozygoptera (which show a zygopteroid type of vesica spermalis) and the Anisoptera are sister groups (synapomorphy box a_1 in Fig. 15d — summarizing mainly the results of ASAHINA, 1954). If the vesica spermalis of the Anisoptera were taken to be primitive, this highly developed structure would have had to have been convergently reduced in the Zygoptera and Anisozygoptera. But up to now there is no evidence for this. Therefore I assume a plesiomorphic correspondence in the vesica spermalis of Zygoptera and Anisozygoptera. **Second** : The sperm-transfer mode of *Epiophlebia* and of the Anisoptera can ***both*** easily be derived from the zygopteroid mode, indicating that the ligula was primarily involved in sperm transfer.

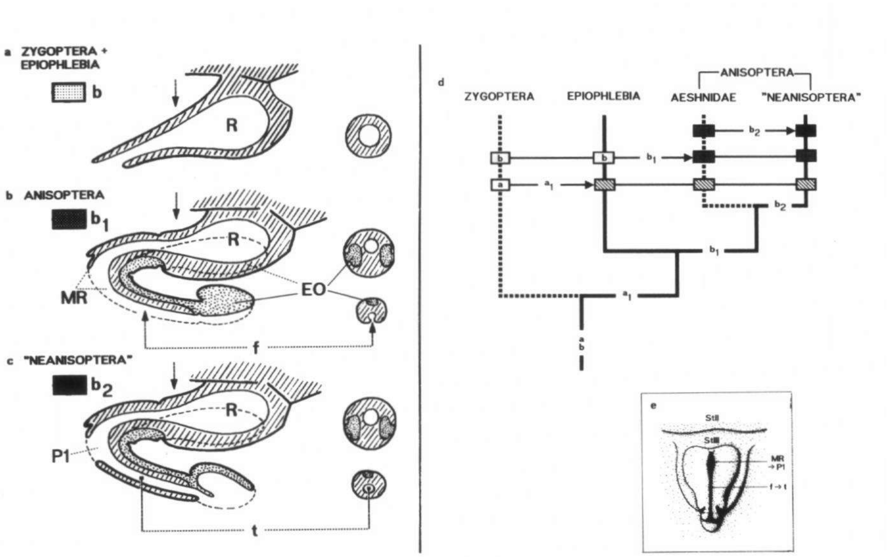

Fig. 15. a-d Phylogenetic evolution ($b\text{-}>b_1\text{-}>b_2$) of vesica spermalis (see text). — "a_1" : synapomorphies of Anisozygoptera and Anisoptera (ASAHINA, 1954 ; HENNIG, 1969, p. 321 ; PFAU, 1971). For the erectile organ (EO ; "Vesica spermalis-Schwellkörper") see also Fig. 17 and PFAU, 1971 (p. 306 f.). In a-c the cross sections of the vesica spermalis on the right side stem from section planes indicated by arrows on the left side. e larval vesica spermalis of a "neanisopteran" dragonfly (*Libellula*).

In **Anisozygoptera** (*Epiophlebia*) this derivation is possible via a hypothetical intermediate stage in which the ligula-penis (L, Fig. 13a, d) of the ancient mode participates together with the hamuli posteriores (HP, Fig. 13b) as a third part in the building of the sperm-channel. Thus an initially incomplete channel formed by the hamuli posteriores was sealed ventrally and frontally.

There is a structure which remained after the complete reduction of the ligula in the anisozygopteran line. This is the so-called processus furculiformis (PF, Fig. 13, 14), together with tiny rudiments of a (sclerotized) connection to the rest of the anterior frame (af). This rudiment strongly indicates the existence of a former functioning ***zygopteroid*** anterior-posterior frame + ligula movement-system in the ancestors of Anisozygoptera (for details of this mechanism see Pfau, 1971 : p. 312 ff.). In addition, a small membraneous lobe (Z, Fig. 13a, d), lying closely behind the processus furculiformis, has been preserved in the Anisozygoptera (Fig. 13b, 14).

In the case of the **Anisoptera** it is very likely that there was an intermediate stage in which the groove of the primitive ligula-penis (fu, Fig. 16a) formed

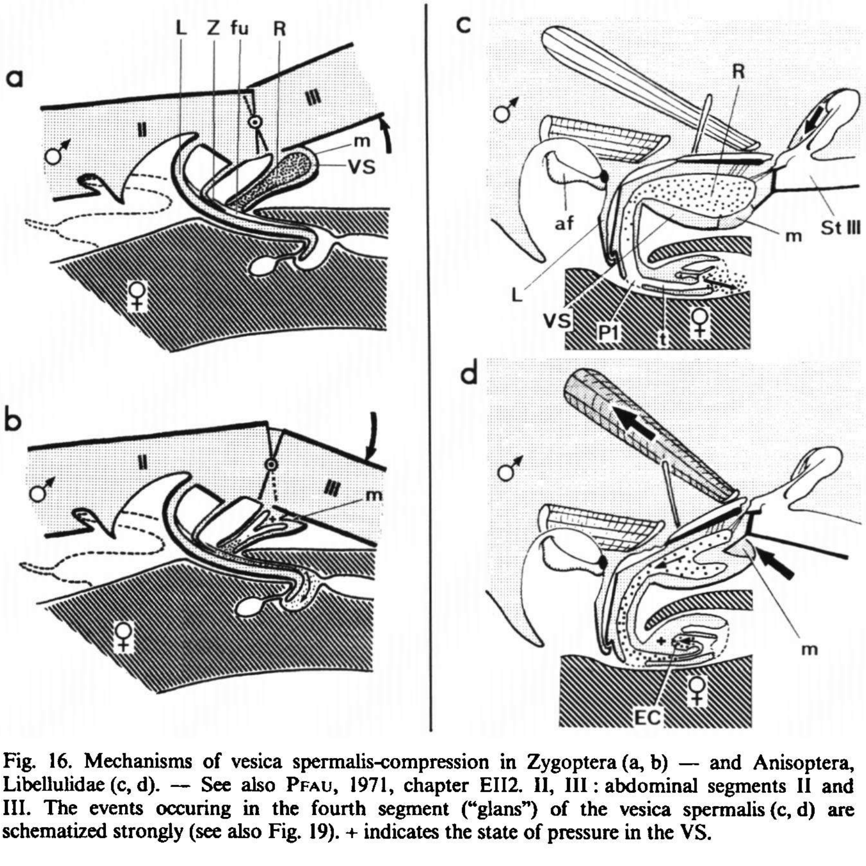

Fig. 16. Mechanisms of vesica spermalis-compression in Zygoptera (a, b) — and Anisoptera, Libellulidae (c, d). — See also Pfau, 1971, chapter EII2. II, III : abdominal segments II and III. The events occuring in the fourth segment ("glans") of the vesica spermalis (c, d) are schematized strongly (see also Fig. 19). + indicates the state of pressure in the VS.

a tube together with a groove (f, Fig. 15b) of the now prolonged, and downwardly and caudally bent vesica spermalis. In a further stage of development the vesica spermalis-groove was almost completely closed (the small slit that stayed open can still be found in the extant Aeshnidae ; Fig. 17). The ligula, during this process of transformation became progressively released from the function of sperm transfer and was turned into a highly developed system for pushing and guiding the vesica spermalis. (It still extends in some extant groups, for instance Aeshnidae and Petaluridae, into the female vagina.) This ligula + vesica spermalis-system of the Anisoptera provides a most reliable synapomorphy of the anisopteran subgroups. The fact that the zygopteroid mode can be converted by reconstruction in all its details into the anisopteroid mode without constraint (PFAU, 1971 : p. 342 ff.) indicates strongly that the evolution must have started from a zygopteroid mode (just as in the case of Anisozygoptera).

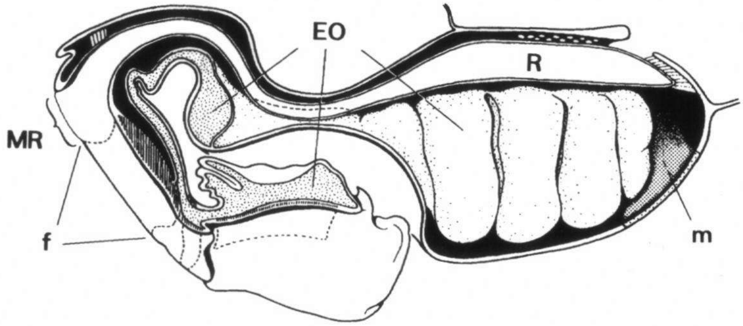

Fig. 17. Vesica spermalis of *Aeshna* (longitudinal section). — The filling-porus "MR", lying proximally to a furrow ("f"), is (in contrast to the "P1" of "Neanisoptera" — and also to the "MR" of Zygoptera) not a real porus.

There is no doubt that the copulatory apparatus of the Anisoptera is most strongly derived. In certain aspects it is also the apparatus with the highest developmental potential, since here the vesica spermalis, the organ of sperm storage, became the "penis" itself. Taken by itself (i.e. without the ligula — if the primitive vesica spermalis alone had been only elongated) the vesica spermalis would not have been suitable for the evolution of a functional penis, since it points in the wrong direction. However, as a flexible organ and in co-operation with the ligula all the necessary new functions could be achieved, while maintaining the essential older functions, for instance the function of sperm-loading into the reservoir (PFAU, 1971 : p. 322 f.).

Although these arguments strongly support the assumption that the zygopteroid mechanism of sperm transfer is plesiomorphic, this does not necessarily imply that the zygopteroid apparatus is primitive as a whole. "Primitivity as a whole" would mean that the apparatus of the Anisozygoptera and Anisoptera would have been developed from a state just as represented in the extant Zygoptera. In some aspects, however, the copulatory apparatus of the Zygoptera seems to bear characters which are already advanced and possibly autapomorphous — for instance the complicated mechanism of the anterior frame + ligula, and the ligula itself, which contains a special erectile organ ("Ligula-Schwellkörper", PFAU, 1971 : Abb. 18-20), a convergence with the erectile organ of the vesica spermalis of Anisoptera. These features apparently are very constantly represented in the zygopteran subgroups. Thus the Zygoptera could indeed be a monophyletic group in contrast to FRASER's opinion. The transformations of the zygopteroid apparatus in the lines of Anisozygoptera and Anisoptera therefore probably have started independently from a rather unspecialized zygopteroid state, which, however, is unknown in its details.

One of the most essential problems remains unsolved : are Zygoptera paraphyletic (Fig. 11) or monophyletic (i.e. sister-group of Anisozygoptera + Anisoptera) ? HENNIG (1969) discussed this question intensively (for instance p. 323 f.), pointing out the most interesting aspects of the homologization of the different cercal apparatuses, and the consequences which may be drawn, aspects which seem to be important in further attempts to solve this problem as well as for further evaluation of the characters.

Further developments of the vesica spermalis within the Anisoptera. — In Figure 15a the symplesiomorphic vesica spermalis of the Zygoptera and Anisozygoptera is illustrated (symplesiomorphy-box "b" in Fig. 15d). The derived vesica spermalis "b_1" of the Anisoptera shows further developments in its subdivision into four elements and also in the existence of a hydraulic erectile organ (Fig. 15b, c ; EO = "Vesica spermalis-Schwellkörper" of PFAU, 1971). In some aspects the vesica spermalis remains plesiomorphous in the family Aeshnidae, where it still carries a furrow (f), beginning at the level of the lower edge of the filling-porus of the vesica spermalis (which maintained approximately its primitive position). This furrow can be considered as a part of the primary zygopteroid filling-porus, which in principle has been much elongated together with the vesica spermalis. The aeshnoid stage of the vesica spermalis is symbolized in Fig. 15b, d with the apomorphy-box "b_1" of Anisoptera. But within the Anisoptera this stage is a clear plesiomorphy, since all the other Anisoptera developed the vesica spermalis further and completely closed the furrow "f" within a distinct section to form a tube "t" (apomorphy-box "b_2" ; Fig. 15c, d). In these Anisoptera — which are designated here (preliminarily, see below) as "Neanisoptera" — the primary furrow of the anisopteran vesica spermalis still exists in the last larval stage (Fig. 15e) — a nice ontogenetic recapitulation of its former appearance. But there are still some doubts that this derived vesica spermalis "b_2" is a true synapomorphy of non-aeshnoid Anisoptera.

The Aeshnidae up to now have been defined only by plesiomorphies and therefore are not necessarily a monophyletic group (notice the dashed line in Fig. 15d — just as in the case of the Zygoptera, Fig. 12). New results of SIVA-JOTHY (unpublished), concerning the ultrastructural anatomy of spermatozoa and spermatodesms possibly indicate autapomorphic characters of Aeshnidae. If the Aeshnidae and "Neanisoptera" could be confirmed as monophyletic groups, the Aeshnidae could be designated as the "Palanisoptera".

The doubts concerning the monophyly of the group, "Neanisoptera", depend crucially on further evaluations of a special character of the vesica spermalis, the sperm-chamber in its fourth segment. This sperm-chamber is in principle a dilatation of the bottom of the distal continuation of the groove "f" (AK, EC; Fig. 16c, d, 18, 19). Figure 15b and 17 show medio-sagittal sections of the vesica spermalis of Aeshnidae: there is no sperm-chamber in the Aeshnidae, the sperm-chamber existing only in non-aeshnoid Anisoptera.

The sperm-chamber of the fourth segment of the vesica spermalis of non-aeshnoid Anisoptera certainly plays an important role in the expulsion of the sperm out of the reservoir. During this process (in all Anisoptera; and in principle in all dragonflies — for Zygoptera see Fig. 16a, b) a rhythmic flexion of the third abdominal segment (respectively sternum) against the second abdominal segment (respectively sternum) compresses and re-expands a proximal membraneous part of the vesica spermalis (m; Fig. 16, 17). Since the sperm-chamber is directly adjacent to the hydraulic erectile system (EO), abdominal (respectively sternal) flexion not only compresses the sperm-reservoir but also puts the sperm-chamber under pressure (by the compressed erectile organ), after which the pressure is released (the state of pressure is indicated by the +-signs in Fig. 16d, 18b, d and 19b). Thus the chamber probably works as a distal suction and pressure pump of the vesica spermalis: it aspirates sperm from the reservoir and then pumps it into the vagina of the female (see arrows).

In two groups of non-aeshnoid Anisoptera, however, the Petaluroidea (= Petaluridae + Cordulegastridae + Gomphidae) and the Libelluloidea (= Libellulidae + Corduliidae + Macrodiplactidae ? + Synthemidae ?)[3], the function of the sperm-chamber is different. In the Petaluroidea the wall of the distal chamber is pushed into the chamber during the compression of the erectile system (+ in Fig. 18b) and thus the sperm is expelled into the female vagina. When the pressure is reduced the distal chamber is widened again and more sperm is aspired from the reservoir (Fig. 18a). In the Libelluloidea the function of the distal chamber is ***opposite*** to that of the Petaluroidea (at least in the groups studied up to now: Corduliidae and Libellulidae; Fig. 18c, d, 16c, d, 19a, b). In the state of pressure-release the distal chamber is reduced in size

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[3] For possible monophyly of "Libelluloidea" (part. ?) and "Libellulidae" — of which some subgroups still have to be investigated — see PFAU, 1971: p. 340.

by an elastic collapse of sclerites (presumably supported by a bistable mechanism) into the chamber (Fig. 16c, 18c, 19a). Thus the sperm is driven out into the female. When the pressure rises (+ in the Figs 16d, 18d, 19b), the chamber is widened against the elastic forces of its wall and sperm is then sucked in from the reservoir.

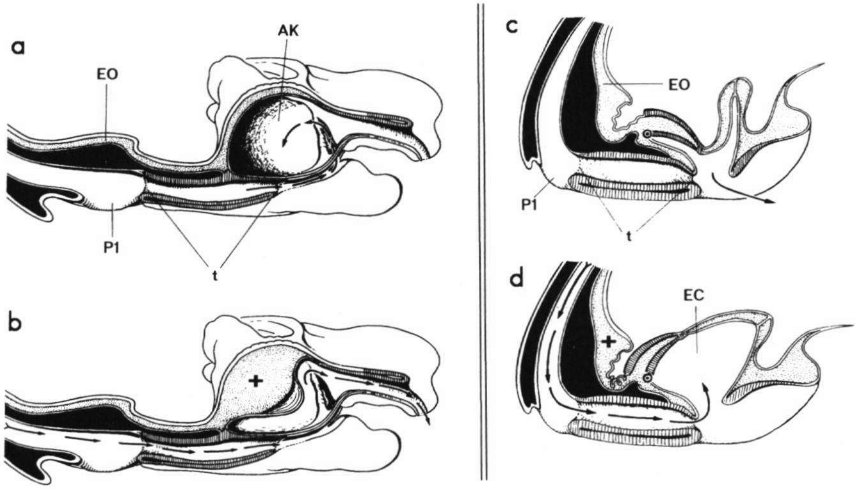

Fig. 18. Different suction-pressure pumps of the vesica spermalis of "Neanisoptera": (a, b) Petaluroidea (*Cordulegaster*) ; — (c, d) Libelluloidea (*Cordulia*). — See text. — The margins of "P1", the (derived) filling-porus of "Neanisoptera", are membraneous and function like a valve (just as the "MR"-margins in the Aeshnidae ; Fig. 17).

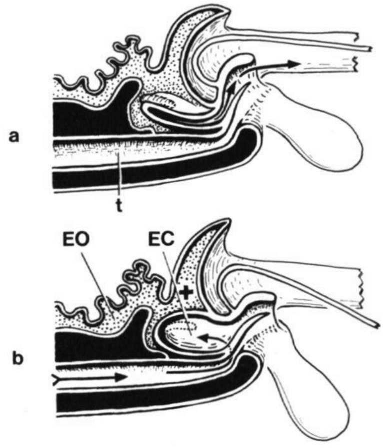

Fig. 19. *Orthetrum* sp., reconstruction of the function of the ejaculation chamber (EC) : (a) "Elastic collapse" causing ejaculation ; — (b) The state of pressure (+) in the EO, effected by compression of the vesica spermalis (Fig. 16d), leads to an extension of the EC, which sucks sperm in from the reservoir (supporting the sperm-flow, effected by compression of the reservoir sac).

There are some interesting differences concerning the efficiency of the two types of sperm chamber (see PFAU, 1971 : p. 349 f.). In addition, whereas in the Libelluloidea only one phase, the phase of vesica spermalis-compression, is sufficient to load the chamber, in the Petaluroidea the loading is in principle bi-phasic, the actual loading of the chamber being in anti-phase to the vesica spermalis-compression (= reservoir-compression). However, in the Petaluroidea the phase in which the strongest anchoring of the vesica spermalis-"glans" in the female vagina occurs (+-phase) is correlated in time with ejaculation ; the total compression force then divides between these two functions, the ejaculation force itself therefore being diminished. The correlation of strongest anchoring and sperm-ejaculation is also to be expected for the primitive Anisoptera ("Aeshnidae", Fig. 17), where (since there is no sperm-chamber) only the primary function of the erectile organ, the spreading out of different structures of the penis' "glans" for anchorage in the female, is accomplished during the phase of reservoir compression. Up to now, however, all these reconstructions of function are hypothetical. Since the special structure of the EC of Libelluloidea indicates mechanisms which are very difficult to understand in detail (for instance : the wall of the EC is by no means homogeneous — Fig. 19), parallel construction and examination of three-dimensional working models are now needed to solve these questions.

Up to now there seems to be no possibility of deriving the mechanism of the sperm-chamber of the Libelluloidea from the mechanism of the Petaluroidea, or vice-versa, since their pumping rhythms are totally opposite. Therefore one cannot decide which sperm-chamber mechanism is primitive and which is derived : each seems to be an autapomorphy of the group in which it is found. This would mean that the distal chamber of the Petaluroidea (AK = "Ausspritzkammer") is not homologous with the distal chamber of the Libelluloidea (EC = "ejaculation chamber").

However, if the distal chambers are convergent structures, we must also reconsider the evolution of the sperm tubes (t) in the non-aeshnoid Anisoptera ("Neanisoptera"). There are two possibilities of intepretation : a sperm-tube could have been evolved in a common stem form of the groups Petaluroidea and Libelluloidea, in order to reduce a loss of sperm, and thus represent a pre-adaptive starting point for the independent evolution of the different distal suction-pressure pumps. This would mean that these two groups are sister groups in a monophyletic group Neanisoptera. The second possible interpretation assumes that the sperm tubes were developed convergently from the primitive aeshnoid furrow, each within its group (i.e. Petaluroidea or Libelluloidea) — in each case together with the development of the distal chamber — in order to improve the effect of suction of the different distal sperm-chambers. If this second interpretation were correct, it would mean that the monophyly of the non-aeshnoid Anisoptera ("Neanisoptera") would be uncertain, since this group was founded only on account of the single apomorphic character "t", the closed sperm tube. Therefore in this case the sister-group relationship between the Petaluroidea and Libelluloidea would also be doubtful. The two branching points (Aeshnidae/Neanisoptera, Libelluloidea/Petaluroidea), which seem to be dependent on each other, therefore need further investigation.

The phylogenetic evaluation of the sperm chambers will depend much on whether an EC can eventually be derived from an AK (i.e. in contradiction to the opinion described here) or not. If a theoretical derivation were possible, the monophyly of the "Neanisoptera" would be corroborated more convincingly ; however for the group Petaluroidea the previously described autapomorphic character AK could then probably represent a symplesiomorphy.

The ovipositor

Comparative investigations on the female ovipositor of Odonata were undertaken to elucidate the phylogenetic relationships within the newly postulated group Petaluroidea.

In the groups Zygoptera, Anisozygoptera and Aeshnidae the ovipositors of the females are primitive, working in an ancient orthopteroid mode : this apparatus is used as a key-hole saw to cut into plant tissue. In Figure 20a the right half of the ovipositor of an aeshnid, which is in its details rather complicated, is illustrated schematically. Figure 20b shows a drawing of the sawing-mechanism, which is very similar (with small changes) in the Zygoptera and in *Epiophlebia.* The strong antagonistic muscles 6 and 7 produce the main sawing movement. Rotating valvifer 2 together with valvulae 2 and 3 around a pivot of (lateral) valvifer 1, causes valvula 2, which is connected to valvula 1 via a sliding joint, to slide back and forth, cutting into the plant tissue.

Within the newly postulated group "Neanisoptera", several interesting alterations of this ancient "sawing-machine" have occurred. The very different apparatus in the genus *Cordulegaster* is shown in Figure 21. Valvulae 1 are characterized by a strong secondary enlargement and cuticular reinforcement (for further details see Pfau, 1985). Leaving aside the extreme elongation, this ovipositor, which has only very few and small muscles, represents an intermediate stage in the evolution of the egg-laying organ of the Gomphidae, not illustrated here. The Gomphidae have only a short vestigial ovipositor ("Legescheide") and even the last muscles have been reduced. Also behavioural and ecological aspects indicate that *Cordulegaster* is a model of a transition stage, since from oviposition into the substrate close to the shore ("planting potatoes" : Fraser, 1957) one can easily imagine a transition to gomphoid ovipositon into open water.

When considering the representatives of the Petaluridae (Fig. 22), an evolutionary sequence can be traced from the cordulegasteroid ovipositor back to the primitive zygopteroid-aeshnoid apparatus. The ovipositor of *Petalura* still shows several relatively strong muscles and a valvula 3, which (in contrast to the valvula 3 of the primitive zygopteroid-aeshnoid ovipositor, which is strongly sclerotized ; Fig. 20a) "starts" to resolve into individual sclerites, which at close inspection can still be found in *Cordulegaster* with a similar positional relationship. It seems as if *Petalura* is an extant missing-link model between the primitive zygopteroid-aeshnoid ovipositor and the cordulegasteroid ovipositor, which enables us to homologize sclerites and muscles in detail.

Behaviour and ecology also in this case are intermediate and support this derivation: the Petaluridae glue their eggs to plants or deposit them into mud (CORBET, 1962). It seems as if valvulae 1 and 2 — and more so valvulae 3 (which have a protective as well as a sensory function) — in this ecological context could "run the risk" of weaker sclerotization.

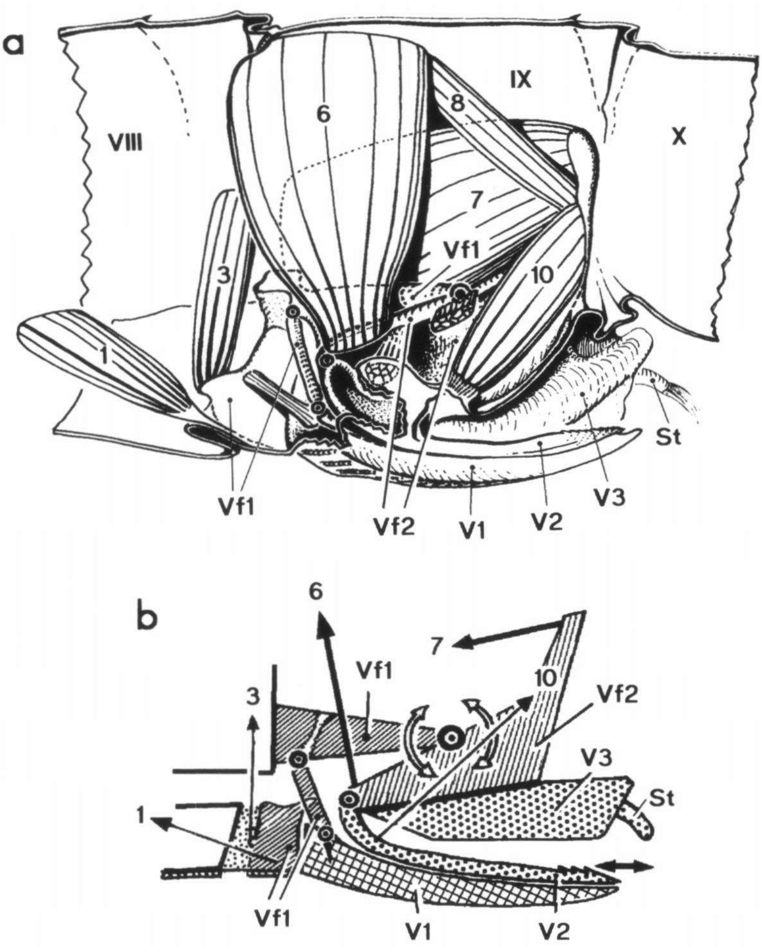

Fig. 20. Primitive zygopteroid-anisozygopteroid-aeshnoid type of ovipositor (*Anax*) and its function. — The right half of the apparatus is seen from the inside of the body. See text. — St : stylus of V3 ; — roman numbers : abdominal segments ; — arabian numbers : muscles.

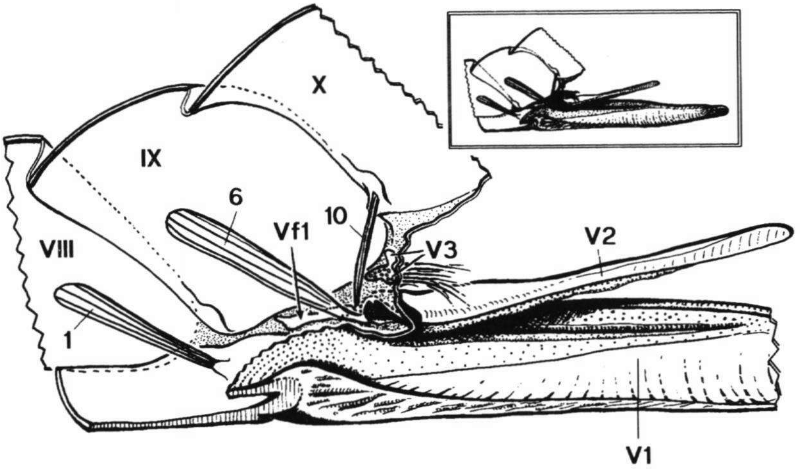

Fig. 21. Ovipositor of *Cordulegaster*. — V1 distally cut (for total aspect of V1, which is ca 7 mm long. see inset). Compare to Fig. 20.

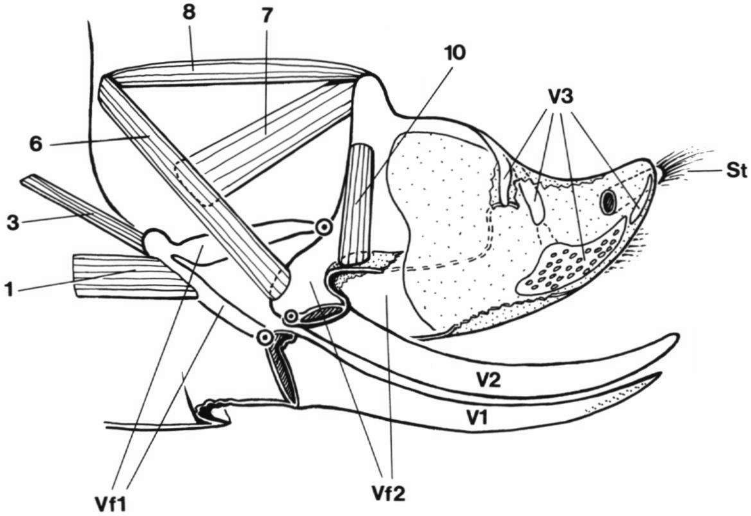

Fig. 22. Ovipositor of *Petalura*. See also Fig. 20 and Fig. 21.

Therefore the Petaluridae — on account of a relatively primitive ovipositor — could be the plesiomorphous sister-group of the Cordulegastridae + Gomphidae. The stem-species of the Cordulegastridae and Gomphidae would then have to be reconstructed such that it could have been the initial stage of the Cordulegastridae as well as of the Gomphidae. These two groups later developed apomorphies of their own (autapomorphies) : there is a strong elongation of valvula 1 in the Cordulegastridae, whereas in the Gomphidae there is an almost complete reduction. The vestigial ovipositor of the Libelluloidea, which is very similar to that of the Gomphidae, is then convergent with the vestigial ovipositor of the Gomphidae.

Of course the reduction of the petaluroid ovipositor in the ancestry of Cordulegastridae and Gomphidae might be also estimated as a convergence, but (following the "principle of parsimony") this possibility has been excluded for the present.

The petaluroid type of ovipositor is interpreted here as being ***relatively*** primitive. In contrast to this it has often been thought of as the most primitive ovipositor of Odonata (based mainly on the study of St. Quentin, 1962). This opinion however is in clear disagreement with Fraser's phylogenetic system as well as with mine.

SOME CONCLUDING COMMENTS

The exploration of the phylogenetic evolution of many groups of insects has reached only a preliminary state today, but some means of advancing the essential phylogenetic reference system seem previously not to have been used sufficiently. A fragmentary state of phylogenetic systematics, however, impedes the necessary evaluation of characters. Since the degree of certainty in character-evaluation depends much on the degree of certainty about the phylogenetic arrangement of the outer groups (i.e. in our special case on questions like : are the Zygoptera para- or monophyletic ? Are the Ephemeroptera a sister-group of the Odonata ? Are the Pterygota monophyletic ?), the mere "formalistic-phylogenetic" approach of "out-group comparison" (Ax, 1988) is often not successful. Additionally it is very vague to postulate synapomorphic correspondences using isolated morphological characters (which are "picked out by accident"), whilst there is only little knowledge about the functional and adaptive value of the "machinery" of which these characters represent a part. Even the most thorough comparative research on isolated structures is unlikely to provide reliable criteria about the direction of evolution or to detect the probabilities of convergence, unless there is information about the functional value and the interdependence of features. It seems very necessary to revive the comparative functional morphology of more comprehensive functional units. (On the other hand in this paper it has been shown to what extent phylogenetic reconstructions can be misled if preceding results are accepted uncritically as "sufficient" — see for instance different former models of the insect flight apparatus.) Results from this field of zoological science are most valuable in phylogenetic reconstructions. Where we succeed in reconstructing uninterrupted lines of evolution (lines without "functional gaps") with the help of research in functional morphology of such comprehensive apparatuses (desirably as complex as the skeleton-muscle systems in this paper), the probability increases, that the evolutionary hypotheses are correct. This may at least be of much help if bigger, seemingly unbridgeable, anagenetic distances exist between groups, where up to now the decision between different possibilities of interpretation was not possible. It has to be kept in mind, however, that these reconstructions are hypothetical and have to be tested by further "reciprocal illuminations", i.e. they have to be checked, corrected and rechecked (Hennig, 1950, 1966, 1982).

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ABBREVIATIONS IN FIGURES

a	anterior pleurum-to-wing joint
A/B	wing stroke axis (defined by joints a and b)
af	anterior frame ("Vorderrahmen")
AK	"Ausspritzkammer" of vesica spermalis
ax1	axillary 1 ("Pterale 1")
"ax4"	"axillary 4"
b	posterior pleurum-to-wing joint
bas(1,2)	basalar muscle(s)
basI,II	basalare I and II
c2	hinge joint between CP* and humeral plate (C2 : axis through c2)
c4	joint on the lower wing surface, between CP* and RAP
C2/C4	axis of forewing forward-movement — running through c2 and c4
CP	costal plate (including humeral plate)
CP*	costal plate (without humeral plate)
dlm	dorsolongitudinal muscle
dvm(1,2)	dorsoventral muscle(s)
EC	ejaculation chamber of vesica spermalis
Ef	epifulcrum (sclerite on the lower RAP-surface)
EO	erectile organ ("Vesica spermalis-Schwellkörper")
f	"furrow" = "open" sperm-duct of the vesica spermalis
fa	fulcro-alar muscle
fu	sperm-furrow of the ligula
HA	hamuli anteriores
hca	posterior coxoalar muscle
Hp	hamuli posteriores
hP	humeral plate
L	ligula
LA	lamina anteriores
LB	lamina batilliformis
m	membraneous area in the (proximal) vesica spermalis
MR	primary filling-porus of the VS (proximal to the furrow "f" in the Aeshnidae)
P1	derived filling-porus of the VS, proximal to the tube "t"

pa	pleuro-alar muscle
PF	processus furculiformis
pf	posterior frame ("Hinterrahmen")
PL	pleural ridge ("Pleuralleiste")
R	sperm-reservoir of the vesica spermalis
RAP	radio-anal plate
StII,III	abdominal sterna II and III
sub(1,2,3)	subalar muscle(s)
T(II,III)	tergum (of meso- and metathorax)
t	tube (closed sperm-duct of the vesica spermalis)
t1	anterior joint of the tergum (to the CP*)
t2	posterior joint of the tergum (to the RAP)
T1/T1	movement axis of Tb (running through left and right joints t1)
Tb	tergal bridge ("Tergalbrücke")
tp	tergo-pleural muscle
V1,2,3	valvulae 1, 2 and 3 of ovipositor
vca	anterior coxoalar muscle
Vf1,2	valvifer 1 and 2 of ovipositor
VS	vesica spermalis
y	pleural joint of Neoptera ("cutting" the basalare I out of the pleurum)
Z	"Zipfel" — membraneous sealing-lobe for L resp. HP

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