

Structure, function and evolution of the 'glans' of the anisopteran vesica spermalis (Odonata)

Hans Klaus Pfau

Rathenaustraße 14, D-65326 Aarbergen, Germany. <clauspfau@web.de>

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ABSTRACT

Comparative investigations of the distal part of the vesica spermalis ('glans') of the anisopteran male secondary copulatory apparatus reveal three different 'solutions' of combining the emptying-mechanism of the sperm-reservoir with a 'washing out' of sperm of the male predecessor. The responsible apparatus of the glans – actually driven by pressure-changes inside the erectile organ, which is a part of the whole vesica spermalis – is shortly apostrophized as 'two-way tap' (Gomphaeschnidae, Aeshnidae), pressure-suction pump (Austropetaliidae, Gomphidae, Petaluridae, Chlorogomphidae, Neopetaliidae, Cordulegastridae) and suction-pressure pump ('Corduliidae', Cordulephyidae, Gomphomacromiidae, Synthemistidae, Libellulidae). The two types of sperm-pump are interpreted to effectuate an intensification of the sperm-jet and to serve as auxiliary devices in emptying the sperm-reservoir. On account of the opposite co-ordination of extension and compression, the two types of sperm-pump are interpreted as alternative; no possibility could be detected to form evolutionary transitions without total loss of functions. This indicates two monophyletic groups: Petaluroidea and Libelluloidea. The phylogenetic relationships between these groups and the Gomphaeschnidae and Aeshnidae remained questionable. The different stages of evolution of the glans, which reflect phylogenetic splittings, are reconstructed. It is assumed that at the beginning a pre-gomphaeschnoid glans (or a gomphaeschnoid 'two-way tap' with tongue?) used two functional pores of ejaculation and scattered sperm on account of the erectile organ-coupled movements of the glans. Advanced glans-types of the Petaluroidea execute a three-phased delivery of sperm portions, the sperm transfer and displacement falling into the compression phase. Instead, in the Libelluloidea the sperm-transmission is two-phased and sperm-transfer and displacement are performed in the decompression phase.

INTRODUCTION

During the last decades the attention on the vesica spermalis of the Anisoptera has increased, mainly because of the phenomenon of sperm displacement in this group (see review of Corbet 2003). This part of the male secondary copulatory apparatus of the Odonata differs considerable within the Anisoptera, especially in its complex distal part, the 'glans' (Schmidt 1915), which should represent the essential part for sperm displacement.

The external structures of the glans have been used as important taxonomic characters for a long time in the range of lower systematic categories. Concerning higher categories, I evaluated (Pfau 1971, 1991) special characters of the vesica spermalis as possibly relevant for the establishment of the groups Neanisoptera, Petaluroidea and Libelluloidea: the sperm tube of the third segment and different types of sperm-pumps inside the glans. The phylogenetic reality of these groups however has been marked with reservation. It was expressed that the character 'sperm-tube' could eventually have evolved independently (convergent closure of the plesiomorphic sperm groove of the third segment) and that the possibility of an evolutionary transformation of one sperm-pump type into the other could not be excluded with certainty.

The phylogenetic grouping of the higher taxa of the Anisoptera has been very controversial subsequently, and several different arrangements of groups have been proposed (e.g. Carle 1995; Lohmann 1996; Misof et al. 2001; Rehn 2003). My phylogenetic groupings have been rejected – obviously my hypothetical arrangement of groups, which was labelled with question marks, was misinterpreted as a definitive result. However, the questions concerning the different types of sperm-pumps have not been pursued. Certainly, Lohmann (1995) drew attention to the existence of closed sperm tubes in the third segment of the vesica spermalis of some Aeshnidae – and also to partially open sperm-grooves in certain Petaluridae (Lohmann 1996: 236, 240) –, which contradict the usefulness of the closed sperm-tube as an autapomorphic character of a monophyletic group Neanisoptera. The existence of sperm-pumps, however, has been denied by this author only by hypothetical guesswork. Proceeding from an apparently different functional morphological base, an alternative interpretation of these structures of the glans as storage chambers for foreign sperm has been attempted; this interpretation has been substantiated by additional hypotheses, which are – without explaining illustrations – difficult to understand. Lohmann used his view for a new phylogenetic arrangement of anisopteran groups.

Miller (1990) even rejected the pure existence of distal sperm-pump like structures in the Libellulidae in a detailed comparative study. This result illustrates very well the situation: obviously no attempt has been made in the meantime, to adequately investigate the glans of the vesica spermalis in its morphological and functional details. Therefore the questions I emphasized in the context of different sperm-pump types have not been solved until now, and the former hypotheses have not been disproved. Since the necessity for new insights is evident, a comparative investigation of the glans has been undertaken, to check the former as well as the new hypotheses, and also to take into consideration possible mechanisms of sperm displacement.

MATERIAL AND METHODS

One of the main problems was, that museum-material of anisopterans consists in most cases of dried specimens. In this material, essential details of the distal part of the vesica spermalis are obscured. Even if it is permitted to withdraw the glans from the animal to look at it from different sides, important connections between its parts remain hidden. This resulted in different homologizations and designations of structures in the past. SEM pictures of the outer appearance are also not of much use, since the degree of sclerotization of the structures, and consequently the presence of joints, is obscured.

To get insights in the functional morphology, the glans of freshly killed animals has been analyzed. Experiments were undertaken to inflate the vesica spermalis ('Entfaltung' of the glans, Schmidt 1915: 163f.). By this, details of the inflation process could be observed directly, the movements of the parts and the existence of joints could be documented. The inflation was managed by squeezing the first segment of the vesica spermalis of a freshly killed anisopteran with a tiny clamp. The proximally squeezed and distally inflated vesica spermalis was immediately preserved and permanently fixed in hot concentrated alcohol for 5 to 10 minutes. This simple method can be performed outdoors with some practice (because alcohol is inflammable, attention is necessary); it is very useful to obtain insights in the construction and function of this complex organ.

For several species only material preserved in Bouin's solution or alcohol was available. This material is ideal for the anatomical study of the deflated vesica spermalis. Using the knowledge from related species, of which inflation-experiments already had been successful, it is possible to infer on the compressed vesica spermalis and glans and e.g. to suggest the presence of joints. For species which only could be studied in dried material, depigmentation of the parts in Chloratren or maceration in KOH was helpful to detect hidden details of organization.

Whereas inflated vesicae spermalis roughly reflect the actions of the glans inside the female vagina, the actual sperm-flow could not be simulated by inflation-experiments. Since previous experiments are judged to be inconclusive (even misleading, cf. Discussion), the sperm-flow – and its possible role with respect to sperm displacement – had to be reconstructed according to functional morphological indications (movement of parts, presence of joints, valves, apertures), by observations in the course of the inflation and by analogy with technical devices.

The drawings in this study are semi-schematic: if necessary certain proportions have been modified for graphic clarity (the diameter of the third segment of the vesica spermalis of Cordulegastridae and Petaluridae e.g. is too large); some components are drawn 'standardized' (e.g. wall and secretion of the erectile organ, hard-sclerotized layers of cuticula, resilin etc.).

Resilin, which was detected in the walls of different sperm-pumps, was identified by its fluorescence in UV-light.

Abbreviations

al	anterior ventral lobe	l-cb	lateral collapsible box
bm	(double) bottom-membrane of SP-p	lev	lever of V4-furrow
bo	bottom-sclerite of V4	l-gr	lateral groove of PS-pump
br	bridge between V3-furrow and external V3-wall	l-lp	lateral lever-process
'c'	'primordial' sperm-pump cavity, part of the j v3-v4	ls	lateral sclerite of process 'f'
cl	claw	m	caudal V1-membrane
co	collar	mb	membranous buffer
col	column	me	membranous region inside the ventral V3-wall
con	connecting structure	m(f)	proximal membranous region of process 'f'
c-ts	cushion of transverse slit 'ts'	m-tg	membranous side-region of tongue 'tg'
dap	dorsal appendage	mpr	median prong
dba	distal balloon	no	nozzle of Pf ₂
d-fil	distal filament	ov	overlap of fur _{v4}
d-fl	distal flagellum	P ₁	filling-pore of the sperm-reservoir
d-fur	dorsal furrow	P ₂	distal orifice of V3-tube (V3-furrow), proximal of processes 'f'
dh	distal horn	pba	proximal balloon
d-m	dorsal membrane of V1	Pf ₁ , Pf _{1*} , Pf ₂	functional pores of ejaculation
dss	dorsal suspensory sclerite	ph	proximal horn
eo	erectile organ ('Vesica spermalis Schwellkörper', Pfau 1971); + compressed; - decompressed	pi	piston
exc	(proximal) excavation of V4-furrow	pl	posterior ventral lobe; in Cordulegastriidae and Neopetaliidae bi-partitioned
f	process 'f' of V3 ('Fortsatz f', Pfau 1971)	p-ps	proximal pump-sclerite
flz(ls)	flexible zone at the base of lateral sclerite 'ls'	psh	proximal shelter
flz(ph)	flexible zone at the base of proximal horn 'ph'	PS-p	pressure-suction pump ('Ausspritzkammer', Pfau 1971)
fur _{v3}	V3-furrow	r	ridge
fur _{v4}	V4-furrow	s ₁ , s ₂ , s _{2*}	seal-points of sperm-ducts and functional pores
gr	longitudinal groove in the medial wall of process 'f'	SP-p	suction-pressure pump ('ejaculation chamber', Pfau 1991)
H	dorso-apical hump of V2	SP-p ₁ , SP-p ₂	proximal and distal pouch of (decompressed) SP-p
h	hook	st ₁ , st ₂	stop-regions of V4-movement
h-f	horn of process 'f'	st3	abdominal sternite 3
j (ls)	proximal joint of lateral sclerite 'ls'	t	V3-tube
j (p-ps)	joint of proximal pump-sclerite 'p-ps'	tg	tongue ('Flagellum', Pfau 1971)
j (psh)	latero-dorsal joint of proximal shelter (between 'psh' and 'l-cb')	tr	triangle
j (s)	secondary dorsal joint between V3 and V4	ts	transverse slit
j st3-v1	joint between abdominal sternite 3 and V1	u	U-sclerite
j v4	joint at the base of fur _{v4} , presumably homologous with j v3-v4	V1-V4	segments of vesica spermalis
j vap-dap	joint between ventral and dorsal appendage	vap	ventral appendage
j vn-vn+1	joints between segments Vn and Vn+1 of vesica spermalis	vba	ventral balloon
		ves	vestibule
		v-fur	ventral furrow of V4
		v-mar	ventro-lateral margin of V3
		vss	ventral suspensory sclerite

STRUCTURE AND FUNCTION OF THE GLANS

Preliminary remarks

Many details of this study are based on former results (Pfau 1971) and will not be repeated in detail – they are picked up again in cases of altered interpretations. This concerns especially structures of the proximal segments of the vesica spermalis and the rest of the secondary copulatory apparatus. Some preliminary remarks are necessary to explain a most important structure inside the vesica spermalis, the erectile organ ('eo' in the Figs).

The erectile organ constitutes in principle an extended epidermal gland without secretion-orifice. Inside the V1 it consists of two sacs on both sides of the sperm-reservoir. The epidermis of the sacs consists of large glandular cells. Because of extensive pleating, the two sacs have a large surface area. Both sacs combine at the base of the V2, forming a small tube, which is surrounded by a thicker cuticular wall, running along the ventral side of the V2 and V3. This tube transmits pressure between the proximal sacs and the glans but presumably allows certain movements of the segments without influencing considerably the internal pressure of the erectile organ. The tube widens distally and occupies the lumen of the glans.

During evolution, in the stem group of the Anisoptera, the simple one-segmented zygopteran vesica spermalis had been prolonged and partitioned in segments. Taking over the role of an intromittent organ ('penis'), the vesica spermalis has been modified distally by differentiation of inflatable and movable regions. The weak point of this system was presumably the ancient zygopteran method of V1-compression, which has been maintained in principle. Because a proximal slit between the V1 and the abdominal lumen cannot be closed totally (passing tracheae, nerves and blood), the loss of pressure through this slit during compression might have been a limiting factor at the beginning of the evolution: on account of this 'leakage', the compression of the V1 – which was strong enough to compress the reservoir and to eject sperm in a zygopteran vesica spermalis – was presumably not sufficiently strong to additionally inflate and move the V4 of the prolonged and more voluminous vesica spermalis. This 'zygopteran deficiency' had been eliminated by evolution of the erectile organ, which can be interpreted as a hydraulic cushion that connects the proximal V1 and the distal glans functionally. Essential new functions in a prolonged vesica spermalis have been enabled by this.

The erectile organ of the anisopteran vesica spermalis is comparable to an inverted hydraulic press, in which a 'large piston', the surface of the sacs, is (indirectly) activated to raise the internal pressure, whereas a 'small second piston', the glans (including the sperm-pump, if present), is quickly moved a relatively long distance. It is expected that the glandular activity of the epithelium of the proximal sacs increases during copulatory activities. On account of this, the erectile organ gets swollen (enlargement of its surface) and its internal initial pressure is increased. According to F (force) = p (internal pressure) \times A (surface of the 'piston'), a smaller force, brought about by the compression of the first segment of the vesica spermalis, will be now necessary to achieve an equal effect as before. The secretory activity of the epidermal cells of the erectile organ should alter the appearance of the glans already in the non-compressed state, since the swelling of the erectile organ represents, in principle, a step in the direction to inflation.

In summary, the active erectile organ can be interpreted as an amplifier. Different (in most cases too low) pressure-states inside this organ are presumably responsible for inconsistent experimental results. These have led to conclusions concerning the sperm-flow, which are incompatible with functional anatomical evidences (cf. next chapters and Discussion).

AESHNIDAE

Boyeria irene (Fonscolombe)

As in other anisopterans, the vesica spermalis of *B. irene* is compressed via a bending-movement of the third abdominal segment in relation to the second segment (cf. Pfau 1971: 331f.). Whereas it is the whole abdominal tergum 3 which is moved downward in relation to the tergum 2, the sternum 3 – which is equipped with an intra-segmental joint ‘j st3-v1’ between the base of the V1 and the abdominal sternite 3 ‘st3’ (Fig. 1) – is erected like a roof in the joints ‘j st3-v1’ (the joints of both sides define a transverse hinge-joint axis), on account of the opposing ligula. The anterior part of the sternite 3 is moved towards the V1 like a piston, compressing a posterior membranous region ‘m’. The increased pressure inside the vesica spermalis leads to (a) a counter-clockwise (as viewed from the left) rotation of V2 (+ V3 + V4) in relation to V1; (b) a clockwise rotation of V3 (+ V4) in relation to V2; (c) a clockwise rotation of V4 in relation to V3; and (d) an inflation of V4; (a) – (c) are indicated in Figure 1 by arrows (for [c] see also Figs 2a–b), (d) in Figures 1 (right) and 2b.

Apart from the movement of V2 (+ V3 + V4) in the proximal joint j v1-v2 – which is apparently the only movement without an amplifying influence of the erectile organ – the reaction of the vesica spermalis to compression is similar to the uncurling of a paper streamer.

The counter-clockwise movement of the V2 is accomplished by the swelling of the dorsal membrane ‘d-m’ of the V1, which operates via a relative large lever to joint j v1-v2 (the joints of both sides define a transverse hinge-joint axis). This movement should play a role at the beginning of the compression: The ventro-caudal movement of the V2 (+ V3 + V4) results in a locking of the dorsal hump (H, Fig. 1) of the V2 in a cavity of the posterior surface of the ligula; this locking improves the resistance of the vesica spermalis against the pumping-movements of the abdominal segment 3.

The clockwise movement of the V3 is accomplished in the joints j v2-v3, which constitute a hinge-joint. The scope of rotation of the V3 ends, when the ventral membrane between V3 and V2 is stretched. This movement, however, cannot take place inside the female vagina. Correspondingly – and in accordance to the locking-device of the V2 in the ligula – the movements of V2 and V3 should be suppressed during inflation-experiments to facilitate the inflation of the V4 (Pfau 1971: 348).

Only the movement of the V4 in relation to V3, again accomplished in a functional hinge-joint (which is poorly defined, since also sideward movements are possible to a certain extent), will play a role in this study. The pivot of this movement is indicated alone in the Figures as j v3-v4; in reality different membranous regions – between the V3-furrow and the V4-furrow and in the ventral external cuticula –

participate in the formation of this joint. In the further text the V4-movements will be designated according to a morphologic correct orientation of the segments of the vesica spermalis as dorsal = upward (during compression of the vesica spermalis) and ventral = downward (during decompression of the vesica spermalis).

When the pressure is raised inside the vesica spermalis by compression of the V1 (cf. above), the thinly skinned sperm-reservoir is compressed and sperm is expelled immediately. In Figure 2a the V4 is shown at the beginning of the compression, not yet inflated and still situated in its lowered position. The sperm however has already passed the filling-pore of the vesica spermalis (P_1 , Fig. 1) and also the sperm-'channel' of the V3 (fur_{V3}) and a narrow 'tube' (d-fur) of the V4. The V4-'tube' obviously prolongs the V3-furrow. It is formed by two narrow grooves, which are situated dorsally in the walls of the V4-furrow (fur_{V4}), separated from the ventral original bottom of the V4-furrow (which is evolutionary older) by a membranous cushion 'lc' along each rill.

It is assumed, that sperm is expelled at the beginning of the compression through a distal orifice of this dorsal V4-'tube', the functional pore Pf_{1*} .

During the further compression the glans is inflated and raised – the latter partly on account of its 'normal' movement (cf. above), and additionally possibly on account of the pressure of the vaginal wall onto the inflating ventral surface of the V4, which raises the V4 passively, as soon as the V4 is pressed against it.

The 'original' V4-furrow (fur_{V4}) is lifted during the upward-movement of the V4. Its proximal end is now brought on a level with the distal end of the V3-furrow and the sperm-flow enters the V4-furrow. Since this furrow forms a bow, which deviates from the dorsal V4-'tube' + longitudinal cushion, the sperm is expelled 'retrograde' (Fig. 2b), leaving the V4-furrow through a projecting, characteristic part (nozzle 'no') of a second functional pore ' Pf_2 '.

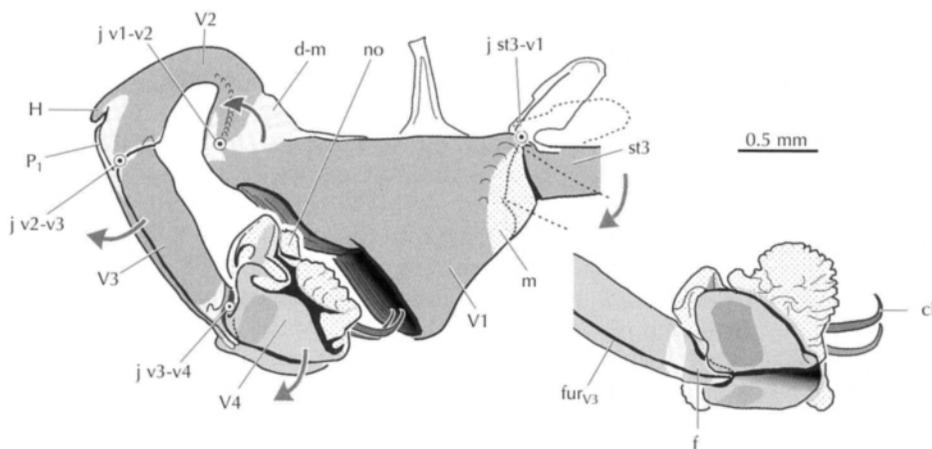


Figure 1: *Boyeria irene* — oblique lateral view of the vesica spermalis; right: inflated V4. The movements of segments V1-V4 – caused by ventral movement of abdominal sternite 3 (st3) and caudal impression of V1 – indicated by arrows. The claws (cl) of the V4 are placed in the resting state well-protected inside the deep, proximally attenuating ventral furrow of the V1. Abbreviations see p. 262.

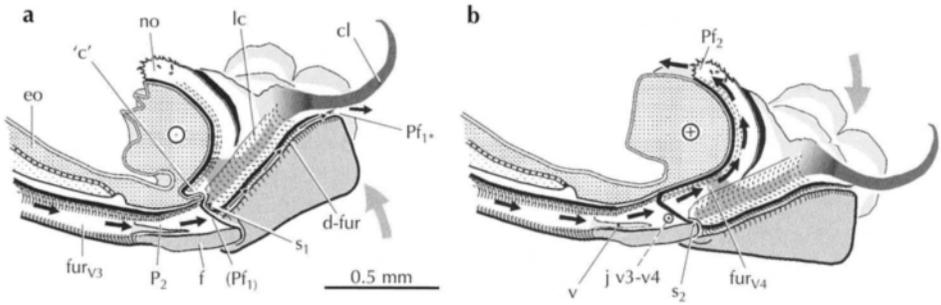


Figure 2: *Boyeria irene*, mediasagittal sections through distal V3 and V4 — (a) beginning compression of the vesica spermalis; (b) maximum compression. Sperm-flow and V4-movements indicated by arrows. The distal edge of the process 'f' and the proximal dorsal wall of the V4 seal the dorsal cleft between V3 and V4 in (a); in (b) the cleft is sealed up by impression of the process 'f' into the proximal region of the longitudinal cushion (lc), constituting the seal-point 's₂'. The jet-valves 'v', in both side walls of the V3-furrow at the height of P₂, can be interpreted as non-return valves. Further abbreviations see p. 262.

The movement-range of the V4 is limited by the soft stops s₁ and s₂, which at the same time represent essential seal-points. Looking at the two extreme positions of the V4 and its different 'channels', the proximal end of the longitudinal cushion 'lc' between the channels either knocks against the ventral or the dorsal edge of the distal end of the V3-furrow. In the ventral V4-position (Fig. 2a) the bowed V4-furrow is pinched off, in the dorsal position (Fig. 2b) instead it is the straight dorsal V4-'tube' which is closed at its proximal end. In the extreme positions the 'at the moment open channel' works exclusively, since the median longitudinal cushions of both sides abut on each other, separating the respective active 'channel' from the inactive one in the full length of the V4.

In a V4-position in between these extreme positions, both V4-channels should be active shortly at the same time, each however diminished.

This whole process of sperm-discharge through different prolongations of the sperm-reservoir + V3-furrow can be interpreted in analogy of a technical two-way tap. Looking at the different directions of sperm-discharge, the retrograde sperm-flow via Pf₂ appears as senseless at first sight. In the context of a 'washing out' of foreign sperm, however, it could be important. The foregoing Pf₁-jet of the own sperm (or of a preceding fluid, respectively) could carry along some foreign sperm, which will then be driven proximally in the direction of the vaginal orifice by the retrograde Pf₂-stream. The ventral wall of the female vagina shows longitudinal rills, which might be important during this 'washing-out action'.

During the following decompression (Fig. 2b-a) the V4 is moved back downwards, executing a wiping-movement, which possibly supports the effect of the foregoing retrograde sperm-jet.

Interesting further structures of the V4 are two strongly sclerotized claws (cl), which are inserted via long rods inside the side-walls of the V4-furrow, visible in their whole length through the longitudinal cushions. The function of these claws is unclear, since they are bowed downwards. It seems possible that the males are

able to modify the movements of the V4 via these claws: each forward or backward movement of the vesica spermalis should lower or elevate the V4, since the claws seem to be able to cling to the vaginal wall. It is imaginable, that either the Pf₁- or the Pf₂-flow of sperm may be suppressed through such 'passive' V4-rotations and that sperm can be expelled (occasionally?) only in the one or the other direction during compression. The normal succession could even be reversed.

It should be mentioned that a further possibility exists to modify the sperm-discharge: if the male would confine the rhythmic compression-movements of the abdominal sternite 3 to small sectors of its total range, theoretically also pure Pf₂- or Pf₁-jets of sperm could be produced.

Further comparisons with species of Aeshnidae indicate, that the combination of the characters 'ventrally bowed claws' and 'presence of a dorsal longitudinal channel (d-fur) along the fur_{V4}-walls' represents an autapomorphic feature (of the genus *Boyeria*).

Aeshna cyanea (Müller)

A successive inflation of the V4 of *A. cyanea* is illustrated in Figures 3a-c. Although the V4 is still situated near to its lowered position in Figure 3b, the V1-compression has already driven sperm distally through the V3-furrow (fur_{V3}). The sperm is seen to be expelled near to the distal end of the V3-furrow through a functional pore Pf₁ (Figs 3b, 4a); the Pf₁ represents a 'false pore', since the rims of the V3-'channel' are not fused dorsally. The V4-furrow (fur_{V4}) is pinched off in this situation by a soft proximal region of its dorsal rim, which is pressed against the ventral end of the V3-furrow (s₁).

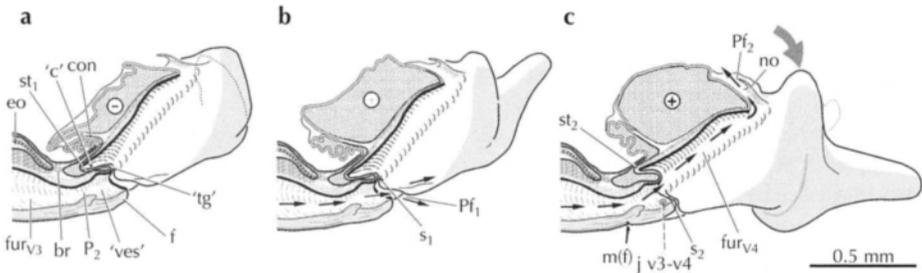


Figure 3: *Aeshna cyanea*, mediasagittal sections through distal V3 and V4 — (a) decompressed V4; (b) beginning compression (reconstructed according to observation); (c) maximum compression. Sperm-flow and V4-movement indicated by arrows; 'tg': point of attachment of the (reduced) tongue; 'ves': 'primordial' vestibule; further abbreviations see p. 262.

As soon as the V4 is elevated a certain distance (c), the soft proximal region of the dorsal rim of the V4-furrow is pressed against the distal end of the process 'f' of the V3. The orifice Pf₁ is now closed (s₂) and the direction of the sperm-flow is changed: The sperm is expelled along the 'channel' formed by the V4-furrow in an oblique ventral direction; since the V4-furrow is bent at its distal end ventro-proximally, the sperm is expelled through a functional pore Pf₂ (Figs 3c, 4b) in a retrograde direction.

The jets of sperm through Pf_1 and Pf_2 are accelerated by a certain device: a short distance proximally of the end of the V3-furrow, at P_2 , the V3-channel is narrowed to a jet nozzle (diameter ca 0.04 mm).

The movement-range of the V4 is limited by soft stop-regions, represented by st_1+s_1 and st_2+s_2 (including 'm(f)'), respectively.

The V4-inflation (Figs 3a–c) and the co-ordinated succession of differently directed sperm-flows in principle correspond to *Boyeria irene*. Therefore again a function of the V4 as a 'two-way tap' – and a washing-out of foreign sperm before depositing the own – is assumed. Compared to *B. irene*, main differences are the absence of claws and of a dorsal furrow (d-fur) in the wall of the V4-furrow.

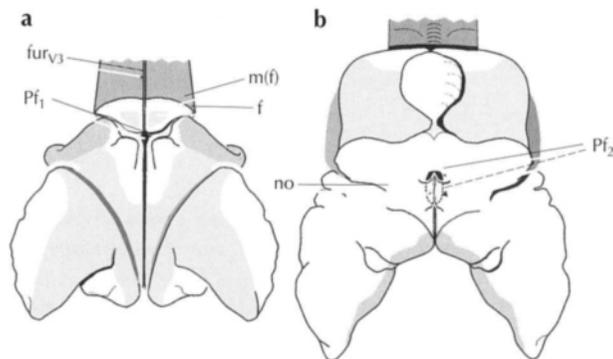


Figure 4: *Aeshna cyanea*, inflated V4 — (a) oblique dorsal view; (b) ventral view. Abbreviations see p. 262.

Several further Aeshnidae – species of the genera *Aeshna*, *Anax*, *Austroaeshna*, *Austrogynacantha*, *Brachytron*, *Caliaeschna*, *Dendroaeshna*, *Hemianax*, *Telephlebia* – have been studied for comparison. The vesicae spermalis of these species, however, could be only studied in the deflated state. Concerning the principal functions of the V4 – ejection of sperm via a 'two-way tap' – all genera should correspond to *B. irene* and *A. cyanea*.

In the genus *Anax* – especially in *A. parthenope* Selys – distinct hollows in the walls of the V4-furrow are present, which are apparently not influenced by the compression of the vesica spermalis. The function of these hollows is mysterious (production of vortices?).

GOMPHAESCHNIDAE

Gomphaeschna furcillata Say

The glans of *G. furcillata* (Fig. 5), which could be only studied in the deflated state, is dorso-ventrally broadened, especially in its apical part, and equipped with a characteristic spiral horn on each side dorsally of the V4-furrow. With respect to its principal construction, this glans also represents a 'two-way tap', but in contrast to the Aeshnidae a tongue (tg) is present as a fundamental seal.

This tongue, which originates from the ventro-apical end of the V3-furrow, is in fact very short, if one considers only the freely protruding distal part. In the decompression-phase (Fig. 5) it is narrowly adjoined to the dorso-basal wall of the V4-furrow, which forms a sharp bend against the rest of the furrow. This transition-

region between V3- and V4-furrow, distally of P_2 , constitutes a narrow channel by a close attachment of the furrows of both sides; it prolongs the V3-furrow and leads to the Pf_1 (' Pf_1 -channel').

During the very beginning of the compression, the tongue should be passively pressed against the ventral wall of the ' Pf_1 -channel' (= dorsal wall of the proximal V4-furrow) by the expelled sperm; this sperm will leave the V4 via the Pf_1 . On account of the dorsal rotation of the V4 during further compression around j v3-v4 (which is poorly defined and allows only a small V4-movement), the Pf_1 should be closed soon: closure of the ' Pf_1 -channel' in its apical part, corresponding to the sealing ' s_2 ' of the Aeshnidae. This V4-rotation, on the other hand, widens the Pf_1 -channel in its proximal part and the flow of sperm should now be able to surround the tongue, which is no longer adjoined to the channel-wall. The sperm of the second part of the compression-phase should therefore enter the narrow V4-furrow (which is broadened laterally) and will be ejaculated via the Pf_2 .

According to considerations that are described in the chapter 'Evolution of the glans', this type of a 'two-way tap' is evaluated as the primitive 'forerunner' of the type of the Aeshnidae.

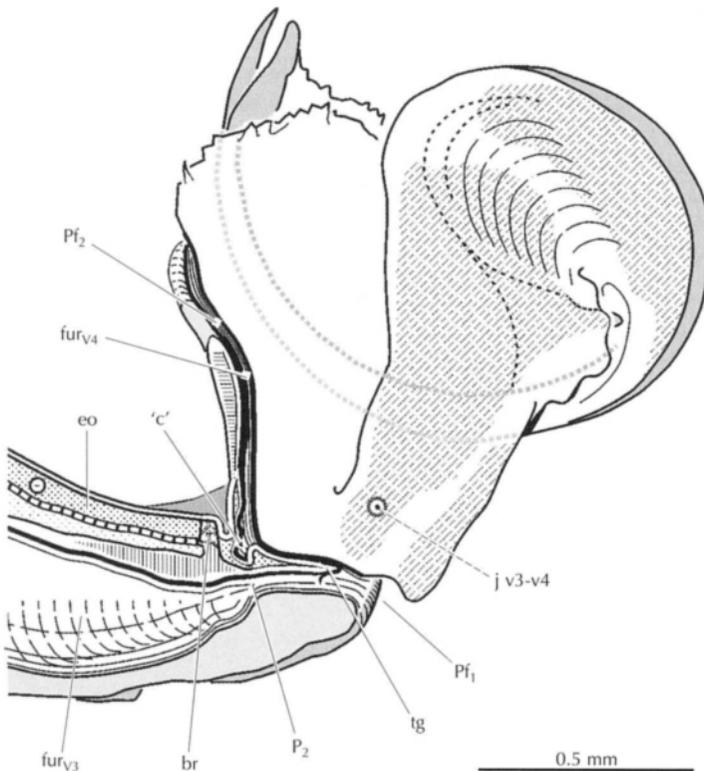


Figure 5: *Gomphaeschna furcillata* — mediasagittal section through distal V3 and (decompressed) V4. In the dorsal region of V4 the sclerites of the lateral side of the base of the coiled horn (which show through) are indicated as hachured areas. Abbreviations see p. 262.

PETALUROIDEA

CORDULEGASTRIDAE

Cordulegaster boltonii (Donovan) and *C. bidentata* Selys

The construction of the glans of the Cordulegastridae is strongly different from that of the Aeshnidae and Gomphaeschnidae:

- Proximally the V4-furrow is differentiated as a large cavity (PS-p, Figs 6, 7), which is extended ventro-proximally and also laterally into an enlarged region of the glans.
- Distal of the (true) orifice P₂ of the closed V3-tube (t), the V3 is prolonged, forming two large processes 'f', which are expanded also ventrally. A comparison with related groups indicates a composite character of the processes 'f' in the Cordulegastridae: an amalgamation of the dorso-apical horns 'h-f' (for these cf. Figs 8-12).
- Inflatable parts of the glans are missing.
- The joint between V3 and V4, the j v3-v4 of the Aeshnidae and Gomphaeschnidae, seems to have been shifted ventrally (j v4), although the strict homology of j v4 with j v3-v4 is uncertain.
- There is a long tongue (tg), which projects from the ventral edge of the end of the V3-tube. Its broadened base is supported by two proximally diverging, sclerotized rods (Fig. 6). Each rod is combined with a projecting structure, which has been designated the 'triangle' (tr), according to its form. This whole arrangement at the base of the tongue is part of a sophisticated system of gaskets that secures the separation and connection, respectively, of two chambers.

The dorso-apical orifice of the PS-pump cavity consists of a broad transverse-slit (ts), which is bordered proximally by the basal structures of the tongue and merges distally into the narrow longitudinal slit-'orifice' of the V4-furrow. In this transition zone, the borders of the transverse-slit (= the dorso-basal borders of the V4-furrow) represent on each side membranous cushions (c-ts). In contrast to Figure 6, the longitudinal dorsal slit of the V4-furrow is normally closed by the tongue, since the tongue is normally situated (and 'arrested') inside the V4-furrow near to its dorsal borders (cf. Fig. 7 and below).

The PS-pump cavity is flanked latero-distally on each side by a dorso-ventrally extended solid element, the column (col). These columns combine the region of the bottom of the PS-pump cavity with the base of the tongue. Each column shows a rather robust sclerotization mainly in the dorsal region, which merges into the sclerotization of the triangle. The two columns serve as abutment-elements of the up- and down-movements of the V4, since each column ends ventrally near to the joint-region 'j v4'. Both joints define a transverse hinge-joint axis.

The dorsal rims of the V4-furrow are undulated, roughly corresponding to the undulating ventral rims of the processes 'f'. However, the functional dorsal border of the V4-furrow is situated below this dorsal margin: on each side it is represented by a longitudinal, medially protruding ridge in the wall of the furrow, which is indicated by a line 'r' in the Figures. The function of these ridges is to keep the tongue in place, i.e. to ensure that the V4-furrow is sealed dorsally. Proximally the

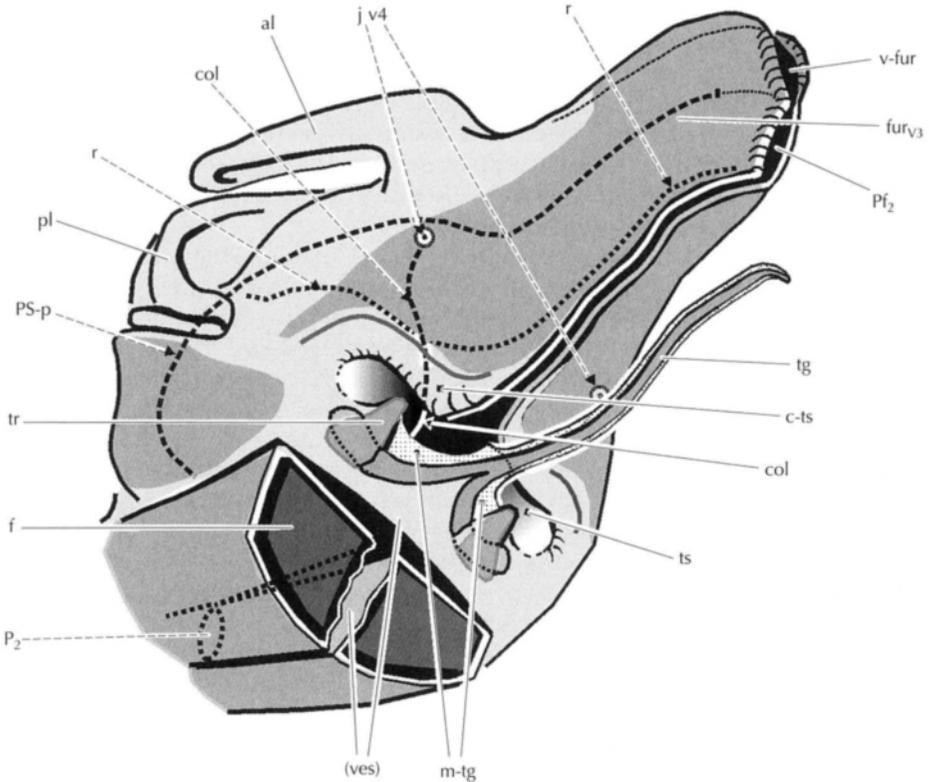


Figure 6: *Cordulegaster* sp. — oblique ventral view of the decompressed glans. Processes 'f' of V3 cut slightly distal of P_2 ; tongue (tg) dragged out of the V4-furrow, to show the transverse slit 'ts' and the dorsal end of the left column 'col'. Abbreviations see p. 262.

ridges enlarge, crossing the columns (col) medially. From there on a groove is formed lateral to each ridge, which ends inside the cavity. These grooves, which exist on both sides, are designated as the lateral grooves (l-gr) of the PS-p.

The margin of the tongue consists of a thin membrane (m-tg) on each side, which appears to contribute essentially to the dorsal sealing of the V4-furrow. This membrane is proximally broadened and attached to the distal tip of the triangle.

The large proximal cavity of the V4-furrow is interpreted as a sperm-pump. Since its lumen is compressed in the compression-phase and widened in the decompression-phase (= resting-position) of the V4, it has been designated as pressure-suction pump (PS-p).

Up to now only reconstructions are possible concerning the actual deformation of the wall of the PS-pump and the actual sperm-flow during compression and decompression (cf. Discussion). During the first compression – partly corresponding to Figure 7b, with the exception of the sperm-portion '3', since the PS-pump cavity is not yet filled – sperm is pressed distally out of the sperm-reservoir, passing the narrow V3-tube 't' and its distal orifice P_2 . This sperm is expected to accumulate mainly between the processes 'f'. Since the medial walls of the two processes are

weakly sclerotized, a 'vestibule' (ves, Fig. 7a) for sperm is formed, which is expandable laterally, representing two adjoining half-chambers. The ventral surface of this vestibule is the dorsal surface of the base of the tongue; it is extended laterally and sealed on each side by the downward-protruding, adjoining lateral region of the process 'f'. Compared to Petaluridae and Gomphidae (see chapters below), the vestibule is poorly defined in the Cordulegastridae. In contrast to Neopetaliidae and Chlorogomphidae (see next chapter) no sign of a specialized distal or dorsal ejaculation-pore (Pf₁) of the vestibule is detectable.

The V4 is elevated in its joints j v4 during compression, moving dorsally around a hinge-joint axis (cf. above). By this, the dorso-apical orifice of the PS-pump cavity (ts, Fig. 6) is closed, since the cushions of its anterior borders (c-ts) are closely pressed against the lamellar regions of the base of the tongue, forming a seal 's₂'* of the PS-pump cavity against the vestibule (Fig. 7b). The triangles (tr) overlap the closed transverse slit, pressing onto the cushions 'c-ts' and securing the lateral regions of the transverse slit.

There is also a (relative small) mobility of the V4 together with the tongue in a flexible region situated proximally of the tongue. In this region the columns and the tongue (which are in sclerotized connection with each other, cf. above) are movable dorsally in the direction of the processes 'f' as a unit. This movement, which is superimposed to the V4-rotation about j v4, is not illustrated in Figure 7.

Two ventral lobes of the V4, the anterior lobes (al), execute a spreading-movement during the compression of the vesica spermalis.

During the following decompression (Fig. 7b→a) the V4 is lowered. The dorso-apical orifice of the PS-pump, the transverse slit 'ts', is now opened – corresponding to Figure 6, the tongue however remaining inside the V4-furrow, beneath the

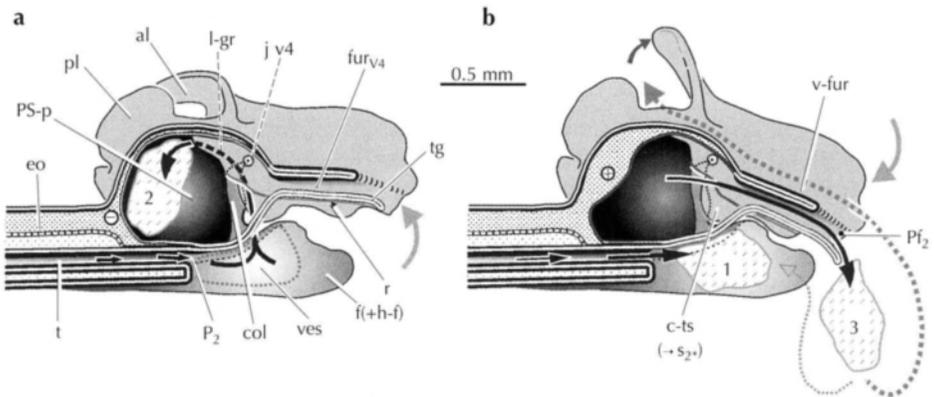


Figure 7: *Cordulegaster* sp. — sagittal sections through distal V3 and V4, slightly parasagittal with respect to the PS-pump, the ventral and dorsal side of which are medially fused to adjacent walls; (a) decompressed glands; (b) compressed glands. Sperm-flow and V4-movement indicated by arrows. Further ways of sperm mass 3 indicated by grey dotted lines (see text). The lateral groove (l-gr), extending lateral of the proximal region of the ridge 'r', is hidden; the triangle (tr, Fig. 6) is not illustrated; 1-3 indicate the three stations of a single portion of sperm ('three-phase sperm-transfer'). Abbreviations see p. 262.

ridges 'r'. Since the elastic walls of the PS-pump are quickly expanding during the decompression (see Discussion), the PS-pump is widened and sperm is sucked out of the vestibule into the pump-cavity. Lateral streams of sperm are supposed to flow ventrally on each side of the base of the tongue, and to enter the cavity, conducted along the columns 'col' and then mainly using the grooves 'l-gr', laterally of the proximal part of the ridges 'r'.

The suction-effect of the PS-pump during decompression should also have some effect on the sperm inside the sperm-reservoir and the V3-tube. It is assumed, that parts of the sperm of the reservoir are sucked distally (cf. arrows in Fig. 7a).

During the next compression (Fig. 7b) the V4 is again lifted and the seal between vestibule and PS-pump cavity is re-arranged. Whereas the vestibule is again filled with sperm from the reservoir, the PS-pump, which has been filled during the foregoing decompression, now expels sperm – just as if one compresses the rubber ball of an enema. The sperm is driven distally, medially of the lateral grooves, and passes the V4-furrow and its distal orifice Pf₂, where the V4-furrow is 'divided' into a left side and right side half-furrow.

The tongue is passively pressed against the ridges 'r' by the sperm in the compression-phase, but does not leave the furrow (cf. above). The dorsal sealing of the V4-furrow is ensured by this in each compression-phase. The result of this solution of the functional problem 'dorsal closure of the V4-furrow' (which has been solved differently in other Anisoptera) is, that tongue and ridges 'r' slide backward and forward in relation to each other during the lifting and lowering movements of the V4 (Fig. 7 a-b).

By alternating compression and decompression the reservoir is successively emptied. Since sperm is probably driven distally in both the decompression and the compression-phase, this type of glans is evaluated as more effective in emptying the reservoir than that of the Gomphaeschnidae and Aeshnidae. Furthermore, sperm, which is driven by a distal pump, is presumably expelled as a strong jet. This jet is directed – on account of the orientation of the V4 and Pf₂ – dorso-apically, in the direction of the female bursa copulatrix. It appears suitable to 'wash out' foreign sperm: since the ventral side of the V4 is excavated, forming a distinct ventral furrow (v-fur) in parallel to the V4-furrow, a part of the sperm should be automatically 'diverted' proximally, in the direction of the vaginal orifice; some sperm may also be diverted along special excavations of the lateral walls of the processes 'f'.

NEOPETALIIDAE AND CHLOROGOMPHIDAE

Neopetalia punctata (Hagen) and *Chlorogomphus brunneus* Oguma

N. punctata and *C. brunneus* will be treated briefly in a single chapter. As in the case of Gomphaeschnidae (cf. above) and Austropetaliidae (cf. below) only a single preserved specimen of each species could be studied.

Aside from differences in development of anterior and posterior ventral lobes, there is a most conspicuous feature of the glans, which separates *N. punctata* and *C. brunneus*, the tongue. The tongue of *N. punctata* is long and well visible between the gaping rims of the V4-furrow (Fig. 10a). It is excavated ventrally, in principle forming a long slender furrow, which 'completes' the V4-furrow to a tube.

The furrow of the tongue is especially deep in its proximal region, where it is extended into two lateral tips (Fig. 8a). This tongue is very similar to that of the Cordulegastridae (Fig. 6), but the proximal tips are more pronounced (in Fig. 7 the proximal tip of the tongue and the triangle are omitted for clarity).

In *C. brunneus* the tongue is short (as in the Gomphidae, Petaluridae and Austropetaliidae, cf. below), constituting a broad lamella which bridges the transverse slit (Fig. 8b; 'ts' not indicated). It is supported by a cuticular zone on both sides and represents, on account of its curvature in the cross sectional plane, a shallow furrow. As in *N. punctata* (and Cordulegastridae), the sclerotized base of the tongue merges on each side into a dorsal sclerotization of the column (col). In spite of its shortness, the seal provided by the tongue in the compression-phase (see Cordulegastridae) is probably sufficient, since the dorsal slit of the V4-furrow is narrow (Fig. 10b; it may even be smaller in the living animal). Therefore only a sealing of the transverse slit at the base of the V4-furrow is necessary.

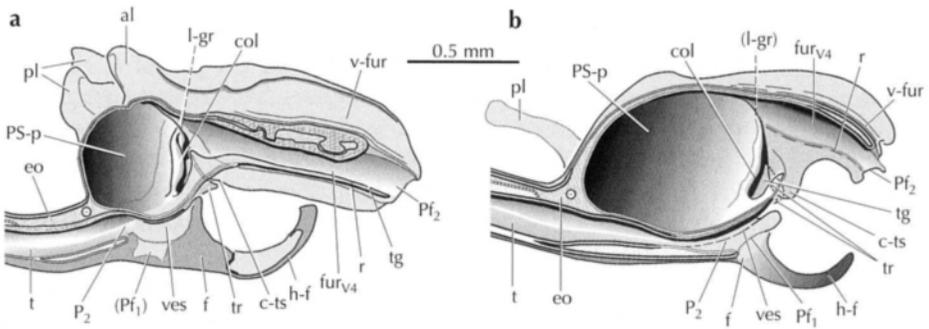


Figure 8: *Neopetalia punctata* (a) and *Chlorogomphus brunneus* (b) — mediasagittal section through distal V3 and decompressed glans. For joint j v4, at the ventral edge of the column 'col', cf. Figs 6 and 7. Abbreviations see p. 262.

The mobility of the V4 (in the j v4 and together with the tongue; cf. Cordulegastridae) is apparently well developed in *N. punctata*; in *C. brunneus*, however, it is only small. In spite of this difference, the principal functions of the glans of the two species should be similar: during decompression the vestibule and the lateral ducts 'l-gr', which lead into the PS-pump cavity, should open at the same time, enabling the sperm to flow from the vestibule into the expanding PS-pump cavity; contrariwise during compression these parts are sealed against one another and the sperm will be ejaculated via the Pf₂.

The morphological correspondences of the essential structures of the glans of the Cordulegastridae, Neopetaliidae and Chlorogomphidae indicate similar functions, which have in principle already been described in the chapter Cordulegastridae. *N. punctata* and (especially) *C. brunneus* however differ in a certain feature, namely in the persistence of a functional pore Pf₁ (Figs 8 and 10). This pore is vestigial in *N. punctata* and has been shifted dorsally, whereas it represents a conspicuous distal orifice in *C. brunneus*. Considering the relative small vestibule of both species,

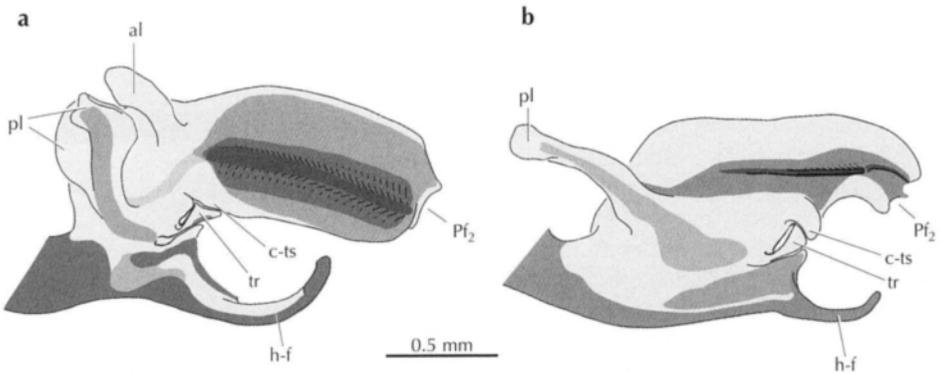


Figure 9: *Neopetalia punctata* (a) and *Chlorogomphus brunneus* (b) — lateral view of distal V3 and glans. Areas of different degrees of sclerotization are indicated by correspondingly different shades of grey. Abbreviations see p. 262.

this character indicates that parts of the sperm are expelled dorso-apically via the Pf₁, especially in *C. brunneus*. During the first compression this will happen as a single event, while in the following compression-phases the Pf₁-jet will occur simultaneous with the Pf₂-jet, which is approximately parallel in *C. brunneus*. It is assumed that also parts of this 'Pf₁-sperm' may be sucked into the PS-pump cavity in the decompression-phases via the transverse slit and additionally via small slits lateral to the triangles (tr, Fig. 9), which should be widened during decompression. The maintenance of a Pf₁ in *C. brunneus* can be interpreted as a relic, which throws light on the succession of structure-function alterations (cf. Evolution of the glans).

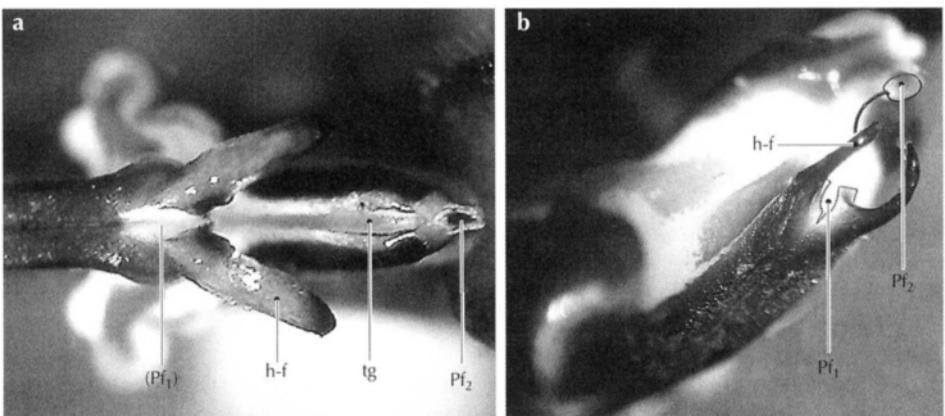


Figure 10: Distal V3 and glans of — (a) *Neopetalia punctata* in dorsal view; and (b) *Chlorogomphus brunneus* in oblique dorsal view. Abbreviations see p. 262.

PETALURIDAE

Petalura gigantea Leach

The principal construction of the glans of *P. gigantea* (Fig. 11) is similar to that of the Cordulegastridae, Neopetaliidae and Chlorogomphidae.

The vestibule (ves) of *P. gigantea* is relative large and very distinct – partly on account of a participation of the base of the tongue, which is ‘hollowed out’ dorsally. This hollow is confluent with a distinct cavity inside the ventro-lateral wall of each process ‘f’. Dorso-apically the vestibule is limited by a collar (co). Since the processes ‘f’ of both sides lie closely side by side, the dorsal slit between the halves of the vestibule should be tight.

As in the Cordulegastridae, characteristic structures between the vestibule and PS-pump are present: the (large) triangles (tr), the columns (col), which are poorly developed and softly sclerotized, and the lateral grooves (l-gr), which represent well developed furrows on both sides, conducting the sperm of the vestibule towards the PS-pump cavity in the decompression-phase (cf. arrow).

The tongue is short and the distal V4-furrow is dorsally practically closed in its full length by bulging membranous borders. The bottom of the V4-furrow represents a thick cushion, consisting of spongy membrane.

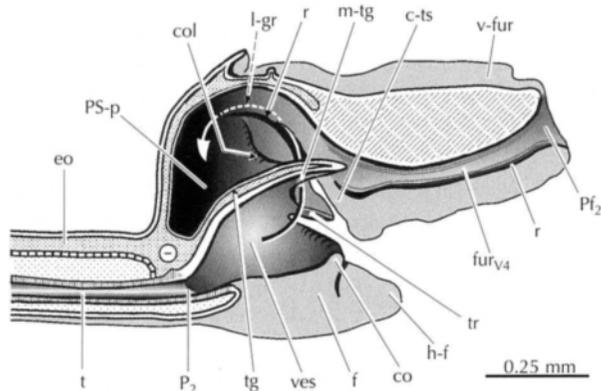


Figure 11: *Petalura gigantea* — mediasagittal section through distal V3 and decompressed glans. Sperm-flow indicated by arrow. The joint j v4, at the ventral edge of the column ‘col’, is not indicated (cf. Figs 6 and 7). Abbreviations see p. 262.

GOMPHIDAE

Gomphus vulgatissimus (Linnaeus)

The glans of *G. vulgatissimus* (Fig. 12) shows a rather small, but distinct vestibule and a relative large PS-pump cavity. The processes ‘f’ are membranous to a large extent and merge proximally into a broad membranous region of the V3 (Fig. 12a). The V4-furrow is closed dorsally, the left side rim overlapping the rim of the right side.

The mobility of the V4 against the V3 is much reduced: only a very small rotation is necessary to close the broad dorsal cleft (ts) between the V3 and V4. Although only preserved vesicae spermalis could be studied, morphological details indicate a lever-mechanism, actuated by a swelling of the ventro-apical part of the V4 during

compression. The V4-furrow should be levered by this swelling dorsally mainly via the strongly sclerotized lateral regions 'lev'. This mechanism is possible because the ventral cuticula, which surrounds the PS-pump cavity, can be deformed in the longitudinal direction and also on account of a certain mobility in a proximal joint-like membranous zone 'me'.

The dorso-basal V4-regions 'c-ts' of the V4-furrow are pressed against distal membranous regions of the processes 'f' during the lifting. This seal corresponds to the 's₂' of the Aeshnidae (cf. Evolution of the glans).

The relative short, proximally broad tongue is supported by two internal, hard-sclerotized rods, which diverge and broaden proximally (cf. the similar construction in the Cordulegastridae, Fig. 6). It is excavated dorsally and participates in the formation of the vestibule, as does also a small proximal region of the V4-furrow between 'c-ts' and 'tg'.

The tongue represents a valve. Principally able to move between two stops – the bottom and dorsal rim of the V4-furrow, respectively (Fig. 12b) – it should function as a non-return valve only when it is lifted. This assumption is based on the fact, that lateral to the tongue passages between vestibule and PS-pump cavity remain open in its lowered position. On the other hand, during compression of the vesica spermalis the jet of sperm of the PS-pump should be stronger than the synchronous jet, which is expelled through the V3-tube. Therefore the tongue is expected to be lifted passively during compression. Only during the first compression, when the PS-pump cavity is still empty, most of the V3-tube sperm will pass the vestibule; this sperm will move the tongue passively downwards and leave the V4 via the Pf₂. During the following compressions, however, the tongue, which is lifted by the stronger jet of PS-pump sperm, should function as a non-return valve, and should additionally hold back most of the synchronous V3-tube sperm inside the vestibule. Since the seal 's₂' between V4 and V3, which is practically closed already during decompression, apparently represents a very close barrier during compression (cf. above), no ejaculation-pore Pf₁ is considered as 'active'.

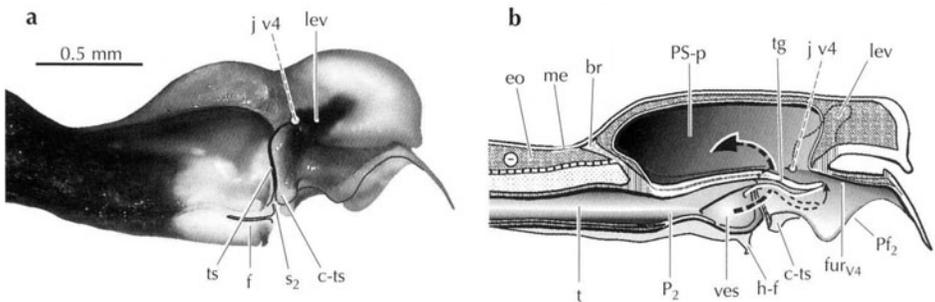


Figure 12: *Gomphus vulgatissimus* — (a) V3 and glans in oblique lateral view; (b) medio-sagittal section through distal V3 and decompressed glans; sperm-flow indicated by arrow. Abbreviations see p. 262.

For investigations of further Gomphidae only preserved material of few genera – *Asiagomphus*, *Actinogomphus*, *Nepogomphoides*, *Onychogomphus*, *Paragomphus* – was available. In spite of many differences in the exterior appearance of the glans, the functional differences are judged to be insignificant. Surprisingly a large difference in the size of the PS-pump has been found in the closely related species *Onychogomphus uncatus* (Charpentier) and *O. forcipatus* (Linnaeus), the latter showing only a tiny PS-pump.

In the Gomphidae several structures of groups described above (Cordulegastridae to Petaluridae) are lacking: the columns, triangles, seal s_2^* and the lateral grooves. Since no vestigial states of these characters have been found in the Gomphidae, and functional considerations indicate that the gomphoid glans is transitional between the austropetaloid and petaluroid glans, the evolution of these structures is interpreted as a late, secondary acquisition in the context of a fundamental transformation (cf. Evolution of the glans). The Gomphidae seem to represent a primitive realization of the glans just at the beginning of this evolution.

AUSTROPETALIIDAE

Archipetalia auriculata Tillyard and *Hypopetalia pestilens* McLachlan

The glans of *A. auriculata* is equipped with a relative small PS-pump (Fig. 13b), but is otherwise much different from the glans of the groups treated above that possess a PS-pump.

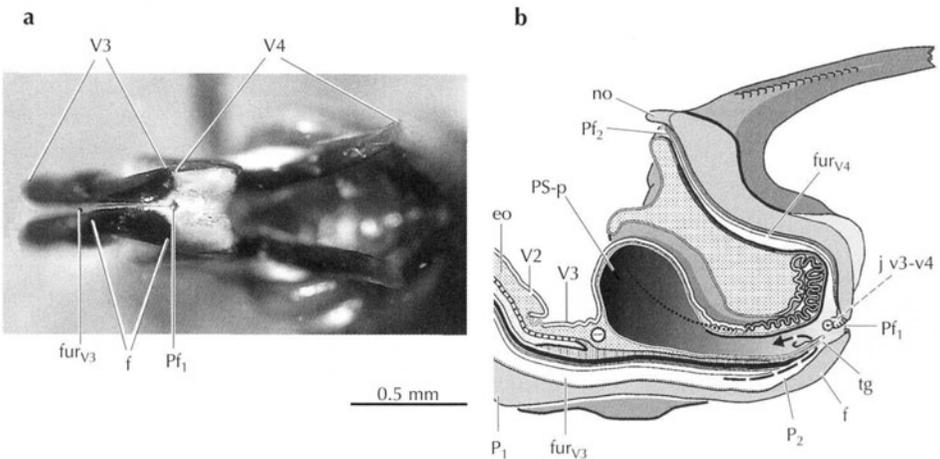


Figure 13: *Archipetalia auriculata* — (a) vesica spermalis in dorsal view; (b) mediasagittal section through V3 and decompressed glans. Abbreviations see p. 262.

The V4 is movable in a typically situated aeshnoid joint-region (only the pivot of this joint is indicated as 'j v3-v4'), which allows an extremely large upward movement – presumably more than 120°. The much pleated external ventral cuticula of the joint is extended during the dorsal movement of the V4. This region shows a very high elasticity, which is even obvious in the preserved glans. Since the large, bowed distal horns of the V4 are rather stiff (mainly at the base), it seems unlikely that the whole play of movement is used inside the female vagina. Instead it is likely that the V4 is passively moved on account of its horns in dorsal direction as soon as the male tries to push its vesica spermalis into the vagina. So, the glans should lie inside the vagina in an 'erected' state, the horns adjoining the dorsal wall of the vagina, the tips of the horns pointing in the direction of the vaginal opening.

In spite of this 'restricted situation' inside the vagina, a certain dorso-ventral movement of the glans should be possible during compression and decompression. It should lead to a closing and opening of the Pf₁, similar to the 's₂-Pf₁ mechanism' of the Aeshnidae (Fig. 3). However, experiments indicate that the Pf₁ (which is very small: 0.025-0.04 mm) should represent an open orifice at best at the very beginning of the compression-phase; in this moment the sperm will be expelled via the Pf₁- as well as via the Pf₂-pore. Then, as soon as the Pf₁ is closed, during the rest of the compression-phase, the whole sperm will pass the very narrow V4-furrow (smallest diameters ca 0.025 mm) and will be ejected only via the Pf₂. With the exception of the first compression, this jet of sperm should be mixed with sperm from the PS-pump, which has been filled in the foregoing decompression-phase.

During the decompression the V4 is expected to snap back ventrally, performing a wiping-movement (cf. Aeshnidae). The wall of the PS-pump cavity – which is very thin and seemingly not attached to any point of the surrounding cuticula – is widened and sperm of the V3-furrow and reservoir will be sucked into its cavity (arrow in Fig. 13b). Since the Pf₁ opens lately and only shortly during the decompression (if at all), it is assumed that no sperm is sucked into the PS-pump cavity from the vaginal lumen via this pore.

The tongue is short in *A. auriculata*. It is assumed that it separates the sperm-streams, which originate from the reservoir and the PS-pump a short distance distal to the P₂. As in the Gomphidae it should function as a non-return valve of the reservoir (and not of the PS-pump), since the PS-pump is presumably able to produce a quicker jet of sperm.

In *H. pestilens* the tongue is slightly longer and extends to the dorsal base of the V4-furrow. So, in contrast to *A. auriculata*, the PS-pump jet of sperm of *H. pestilens* is conducted across the Pf₁ in the lowered position of the V4 (= at the beginning of compression), improving the separation of the different sperm-streams. As soon as the Pf₁ is closed, these different streams will be mixed, just as in *A. auriculata*.

No indications have been found to confirm the suggestion of Lohmann (1995) that a ventral movement of the tongue against its own elasticity would close the orifice of the PS-pump cavity. It is not clear what force could cause this movement. Moreover: the tongue is unable to seal the PS-pump orifice, since lateral passages remain open (see also Discussion).

LIBELLULOIDEA

The functional anatomy of the glans of the Libellulidae, Synthemistidae and different groups of the 'Corduliidae' shows fundamental differences compared to the groups described before, mainly with respect to the sperm-pump, which differs in the co-ordination of the sperm-suction and -ejection and the compression- and decompression-phases. This different type of sperm-pump is considered as homologous within the groups of the Libelluloidea (cf. Evolution of the glans). Since the Libellulidae and Synthemistidae exhibit peculiarities of the glans, which indicate extensive alterations of a 'corduloid' type during evolution, these most advanced groups will be described at first – corresponding to the ordering of groups in the chapter Petaluroidea.

LIBELLULIDAE

Libellula quadrimaculata Linnaeus

In the resting-position of the glans (= decompressed state, Figs 14a, 15a), the sperm-pump cavity of *L. quadrimaculata* appears compressed in the longitudinal section to two narrow pouches (SP-p₁ and SP-p₂), situated between the distal part of the V3-tube and the V4-furrow. A striking effect of the compression (Figs 14b, 15b) is an expansion of the two pouches into one large cavity 'SP-p'.

Expansion and collapse of the SP-pump are mechanically guided by the movements of a complicated cuticular 'suspensory system', which is situated at the base

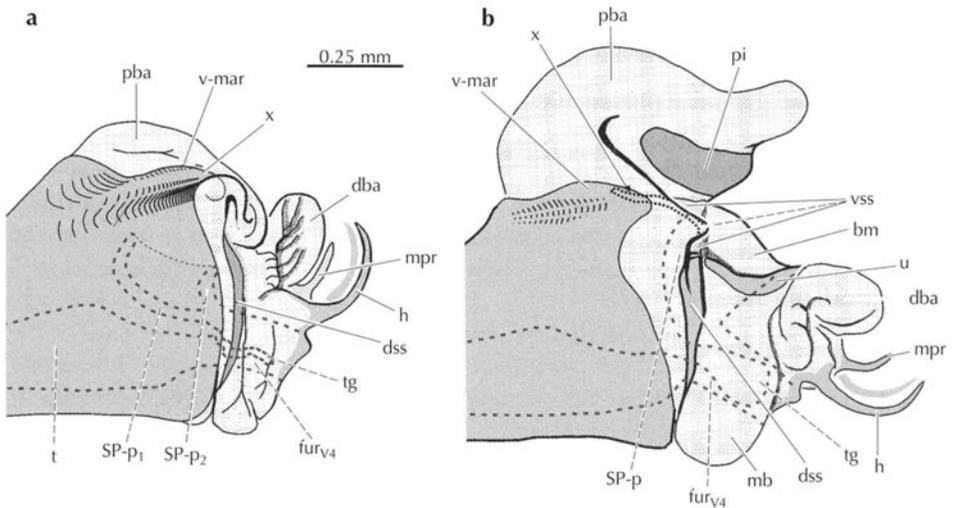


Figure 14: *Libellula quadrimaculata*, lateral view of distal V3 and glans — (a) decompressed glans; (b) compressed glans. In (b) the indication lines for the ventral suspensory sclerite (vss) point to its medial part, to its broad lateral end (articulating at point 'x' with v-mar) and also to the deflected dorso-lateral part (articulating with 'dss'). Abbreviations see p. 262.

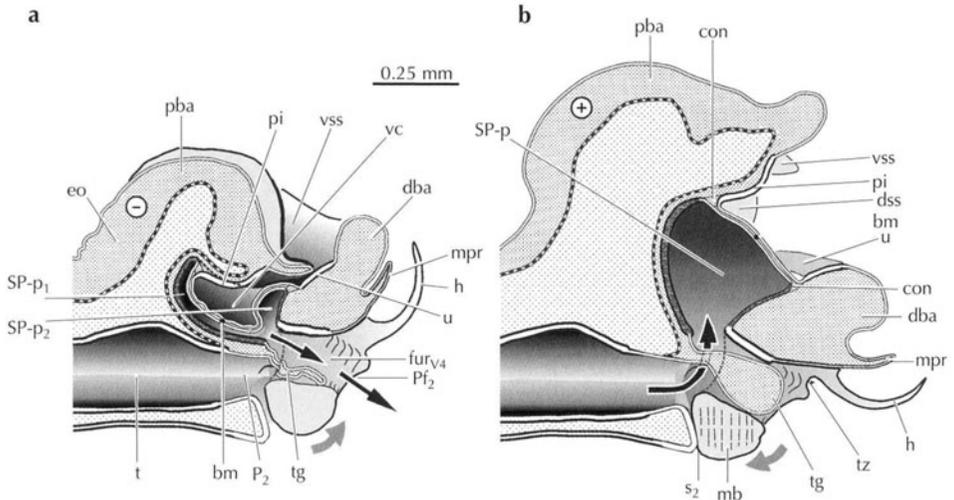


Figure 15: *Libellula quadrimaculata*, mediasagittal sections through distal V3 and glans — (a) partially decompressed glans – in the fully decompressed state the ventral cavity (vc) between SP-p₁ and SP-p₂ is totally suppressed by the sclerite 'pi'; (b) compressed glans. Sperm-flow and V4-movement indicated by arrows; resilin in the wall of SP-p was marked by special texture; 'fz': flexible zone (see text); further abbreviations see p. 262.

of the V4. This system consists of six sclerites (Figs 14, 16): the piston 'pi' – which apparently represents a remnant of the proximal pump-sclerite 'p-ps' of the 'Coruliidae' (cf. Fig. 23) –, the U-sclerite 'u' – which is possibly homologous with the lateral lever-process '1-lp' of e.g. the Synthemistidae (cf. Fig. 19) – and two pairs of lateral sclerites (dss, vss).

Conspicuous external events, which can be observed during the compression of the vesica spermalis, are (1) the inflation of the dorso-proximal region of the rims of the V4-furrow (mb), leading to a closure of the V3/V4-cleft – in addition, the left and right side medial surfaces are pressed against one another; (2) a dorsal movement of the V4, which supports the closure of the V3/V4-cleft; (3) a blowing-up of a very large ventro-distal part of the V3, the proximal balloon 'pba'; (4) the inflation and elevation of a distal part, the distal balloon (dba), combined with the elevation of the V4-furrow and attached distal structures, the median prong (mpr) and the lateral hooks (h); besides this, 'mpr' and 'h' additionally rotate dorsally as a unit relative to the V4-furrow on account of the presence of a flexible zone (fz, Fig. 15b) between these structures; (5) a strong lateral deflexion of the ventral margins of the V3 (v-mar) – this movement is most important for a lateral broadening of the distal V3 (including the SP-pump) and a tensing of an elastic spring; and (6) the inflation of the tongue, which closes the V4-furrow; the V4-furrow represents a functional tube, since it is closed dorsally by its walls, which make contact medially.

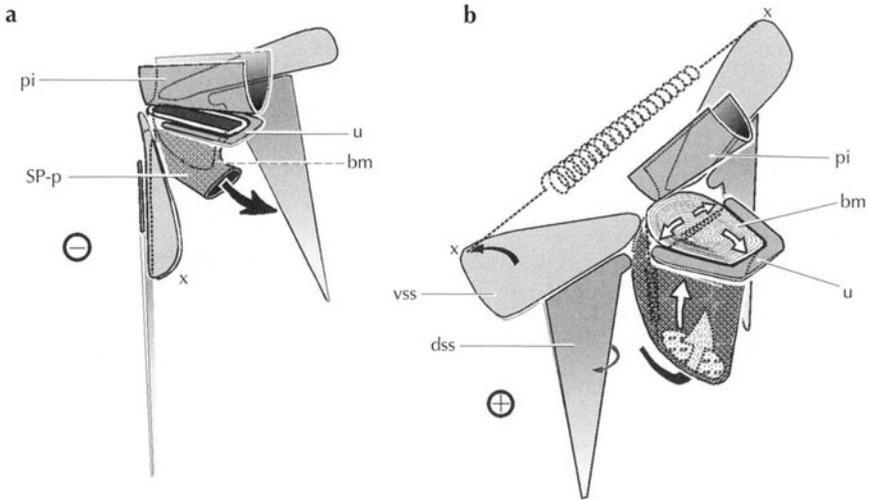


Figure 16: *Libellula quadrimaculata*, schematic drawing of the isolated SP-pump and suspensory sclerites, seen obliquely from latero-disto-ventrally — (a) decompressed; (b) compressed state. Sperm-flow and movements of 'dss' and 'vss' indicated by black arrows; white arrows illustrate the widening of the SP-pump cavity; dotted springs indicate the storage of elastic energy at different places. 'x' cf. Fig. 14. Further abbreviations see p. 262.

Different parts apparently move with different time-constants. The lateral parts of the distal balloon (dba) e.g. are inflated relatively late: expanding laterally and distally and rotating dorsally together with the protuberances 'h' and 'mpr', the 'dba' slowly executes at the same time a curious downward rolling-movement.

The lateral broadening of the distal V3, which is considerable (factor 2), the inflation of the proximal balloon and the elevation and inflation of the V4 are accompanied and mechanically guided by the movements of the suspensory-sclerites (vss, dss, pi, u), which surround the bottom (bm) of the SP-pump cavity; this bottom consists of two adjacent thin layers of integument and is not inflated as a ventral balloon (cf. groups below). The suspensory-sclerites, most of which have been invisible externally in the decompressed state, are spread during compression and come to light like petals of a blossom. This leads to a strong enlargement of the SP-pump cavity.

The joints and movements of the suspensory sclerites are complex: 'vss' and 'dss' e.g. are spread laterally, at the same time moving relative to each other. The events accompanying the SP-pump spreading are illustrated diagrammatically in Fig. 16. It is obvious that the cavity of the SP-pump is not only expanded laterally, but also stretched ventrally and distally. The large expandability of the SP-pump cavity is due to its material: it represents – with exception of its bottom 'bm' (cf. above) – a 'calyx' consisting of thick resilin walls.

The inflation of the glans is illustrated in Fig. 15a-b in mediosagittal sections. The arrows indicate the flow of sperm, which is expected to be sucked into the SP-pump cavity through free passages on both sides at the base of the tongue during compression. It should be mentioned that the dorsal orifice of the SP-pump cavity has been widened during the dorsal rotation of the V4 and inflation of the distal balloon, since these events led to a ventral movement of the proximal part of the V4-furrow – a circumstance which facilitates the inflow of sperm.

The decompression (Fig. 15b-a) is quick and rather dramatic with respect to the SP-pump cavity, which collapses very quickly on account of the release of different elastic springs: the snapping-together of the ventral V3-margins 'v-mar' of both sides, the co-ordinated 'folding' of the suspensory-sclerites and the 'unloading' of the resilin-spring, represented by the SP-pump walls. The sperm is expelled out of the SP-pump cavity during this collapse dorso-distally. The collapsed SP-pump represents now again two narrow 'pockets', SP-p₁ and SP-p₂, in the longitudinal section of the glans.

The tongue deflates during decompression, giving free way to the ejaculating sperm. Furthermore it is moved passively dorsally by the sperm, closing the cleft between V3 and V4 with its broad base.

The presumably strong jet of sperm should be suitable for a washing-out of foreign sperm. Since the proximal balloon (pba) was reduced in size during decompression, together with the folding of the suspensory sclerites and the quick approach of the 'v-mar', a retrograde passage is free for washed-out sperm.

In accordance to the different time-constants of movements (cf. above), the distal balloon seems not to be deflated completely during the decompression. Especially its lateral parts, which inflated late during compression, may therefore continue to serve as anchorage-elements.

Orthetrum cancellatum (Linnaeus)

The glans of the vesica spermalis of the genus *Orthetrum* Newman has been investigated to check the results of Miller (1990), which strongly contradict Pfau (1971, 1991). Miller's investigation is based on *O. coerulescens* (Fabricius) and had been generalized in essential details for the Libellulidae. *O. coerulescens*, however, could only be studied in its decompressed state. Since this species is very similar to *O. cancellatum* (Figs 17, 18), all results made on *O. cancellatum* should also apply to *O. coerulescens*.

O. cancellatum exhibits, compared to *L. quadrimaculata*, some remarkable differences:

- The appearance of the SP-pump is different in the folded (= decompressed) glans (Fig. 17a). Whereas in *L. quadrimaculata* longitudinal sections show a relative thin cavity bottom situated between two narrow pouches of a resilin-walled 'calyx', the anterior part of this calyx (SP-p₂) is reduced in *Orthetrum*: anterior cavity wall and cavity bottom (bm) are confluent in approximately straight line.
- Two pairs of appendages are present: The dorsal appendage (dap) represents a protuberance of the rim of the V4-furrow; the 'dap' is possibly homologous with the 'dh' of the Synthemistidae and further groups (cf. below) – its ventro-basal region is possibly homologous with the 'dss' of *L. quadrimaculata*. The

ventral appendage (vap) is proximally ramified into two branches. The dorsal branch (its base seems to correspond to the 'vss' of *L. quadrimaculata*) participates proximally in the formation of the 'j vap-dap', a joint between the ventral and dorsal appendage (Fig. 18c); the ventral branch merges into the ventral margin of the V3.

- There is a very long single distal filament (d-fil); this filament is possibly homologous with the short median process 'mpr' of *L. quadrimaculata*. Vestiges of the sclerites 'pi' and 'u' are detectable; 'pi' is indicated in Figure 18c.
- The structure of the SP-pump is complex (not illustrated). In the resting state the left and right side parts of the pump are extended dorsally beyond the V3-tube (t), which is therefore nestled in between two pump-halves. Laterally the wall of the SP-pump is attached to the joint 'j vap-dap', between the ventral and dorsal appendage. Strongly moved disto-latero-ventrally during compression, these left and right side points of attachment are essential for the spreading of the SP-pump cavity. The wall of the SP-pump is highly differentiated, showing different diameters of resilin in different regions (Pfau 1991: 134).
- The V4-furrow is dorso-proximally linked to the distal end of the V3 via a distinct joint 'j (s)'.

Figures 17 and 18 show that all appendages are moved during compression: the ventral appendages (vap) are spread ventro-laterally, whereas the dorsal appendages (dap) and the distal filament (d-fil) are at the same time rotated dorsally together with the V4-furrow, which is moved in its proximal joint 'j (s)', executing the 'normal' dorsal V4-movement. These movements of the ventral and dorsal appendages and the V4-furrow are mechanically coupled. On account of this, the system can be spread and the SP-pump widened (to a certain extent) by moving only one of these parts in the decompressed V4 in experiments. The dorsal movement of the V4 is at the end, when the 'dap' reach a stop at the dorso-apical margin of the V3 (Fig. 18b). The base of the distal filament is not only rotated dorsally together with the V4, but additionally displaced to the V4-tip, since the ventral part of the V4-furrow is extruded during compression; in its inflated state the distal region of the V4 forms a laterally broadened surface (Fig. 18c). During this abrupt inflation of a (vestigial) distal balloon, which occurs late during compression, the distal filament is moved vigorously and whip-like.

As in *L. quadrimaculata*, the ventral borders of the V3 (v-mar, Fig. 18a) are spread strongly laterally, leading to a considerable broadening of the V3 (by a factor of 3.5). This deflexion of the ventral V3-margins is again essential for the stretching and lateral broadening of the sperm-pump cavity. Similar to *L. quadrimaculata*, these lateral regions of the V3 are most essential for storage of elastic energy and for a sudden SP-pump cavity-collapse during decompression, working together with the elastic spring represented by the resilin-walls of the pump itself.

The proximal balloon (pba), which forms a protective collar of the V4-furrow in the decompressed state (psh, Fig. 17a), executes a curious movement during compression: while inflating it is at first moved dorso-distally, in parallel with the V4-furrow movement, but then it is moved ventrally. This last movement is a counter-movement in relation to the rotation of the V4-furrow. On account of this, the glans of *O. cancellatum*, including the internal SP-pump, executes a distinctive dorso-ventral spreading during compression.

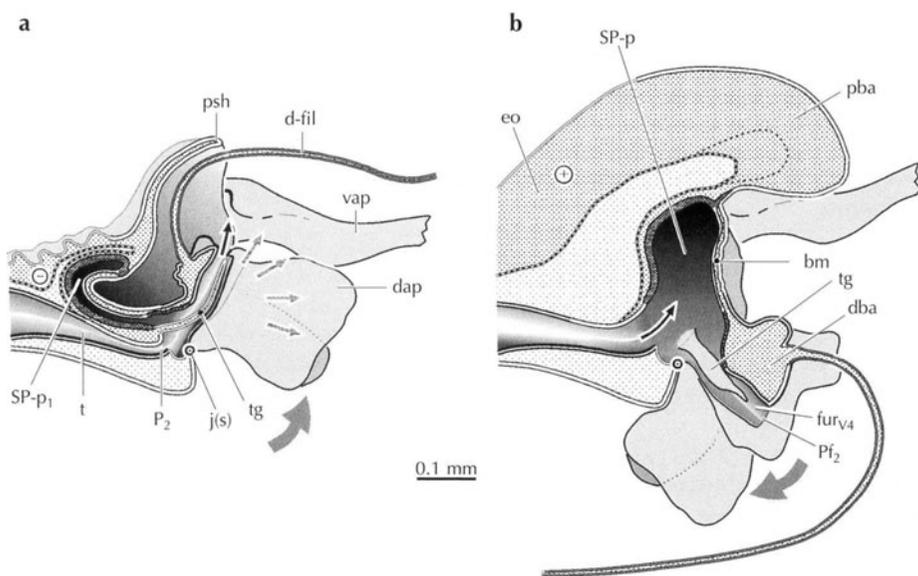


Figure 17: *Orthetrum cancellatum*, sagittal sections through distal V3 and glans — (a) decompressed glans, mediosagittal section; (b) compressed glans, slightly parasagittal section, to show the broadened passage into the SP-pump cavity lateral to the tongue. Sperm-flow and V4-movement indicated by arrows. Hachured arrows in (a) illustrate sperm-scattering during decompression. The lateral walls of the dorsal appendages (dap) are excavated forming external furrows, which might be important for a proximally directed flow of foreign sperm during decompression. The distal filament 'd-fil' and right ventral appendage 'vap' are cut. In (a) the ventral appendage shows a medio-basal indentation, into which the lateral rims of the deflated proximal shelter 'psh' fit. Abbreviations see p. 262.

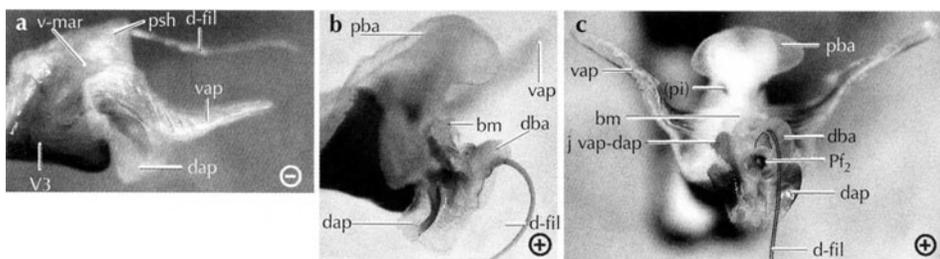


Figure 18: *Orthetrum cancellatum* — (a) decompressed and (b) compressed glans in lateral view; (c) compressed glans in oblique distal view. Abbreviations see p. 262.

The proximally broad, long tongue (tg) is inflated during compression as in *L. quadrimaculata*; therefore the main function of this structure can be seen in the closing of the V4-furrow in the compression phase. Since the dorsal cleft between V3 and V4 is totally closed at the proximal end (at joint 'j (s)') – and the V4-furrow is practically closed dorsally (its rims are even fused in the proximal region in *O. coerulescens*) – only the way into the SP-pump cavity is free for the sperm during compression.

During decompression the tongue functions as a non-return valve: it is deflated and passively pushed dorsally by the ejected sperm, thus preventing sperm from being expelled back into the V3-tube. With respect to the sperm-flow, the events should in principle correspond to those described for *L. quadrimaculata*. As shown by arrows (Fig. 17a), the sperm is scattered widely during decompression in *O. cancellatum* on account of the comparatively large ventral movement of the V4-furrow.

SYNTHEMISTIDAE

It was not possible to investigate inflated vesicae spermalis of synthemistid anisopterans. According to this, the main events of the inflation of the tiny glans' of the Synthemistidae had to be reconstructed, making use of experiences from previously treated groups.

Whereas the secondary copulatory apparatus of the Synthemistidae turned out to be largely of a primitive-corduloid type, its vesica spermalis is strongly discrepant: the glans exhibits very advanced features that appear partly libelluloid and partly autapomorphic.

Choristhemis flavoterminata (Martin)

In *C. flavoterminata* the dorsal rims of the V4-furrow are equipped with large projections, the distal horns (dh, Fig. 19). The processes 'f' of the V3 are large and fused. In the side region of each process a distinct three-cornered lateral sclerite 'ls' is differentiated, which articulates latero-basally via a joint 'j (ls)' with a projecting region of the V3 – lateral to a pair of protuberances, the proximal horns (ph).

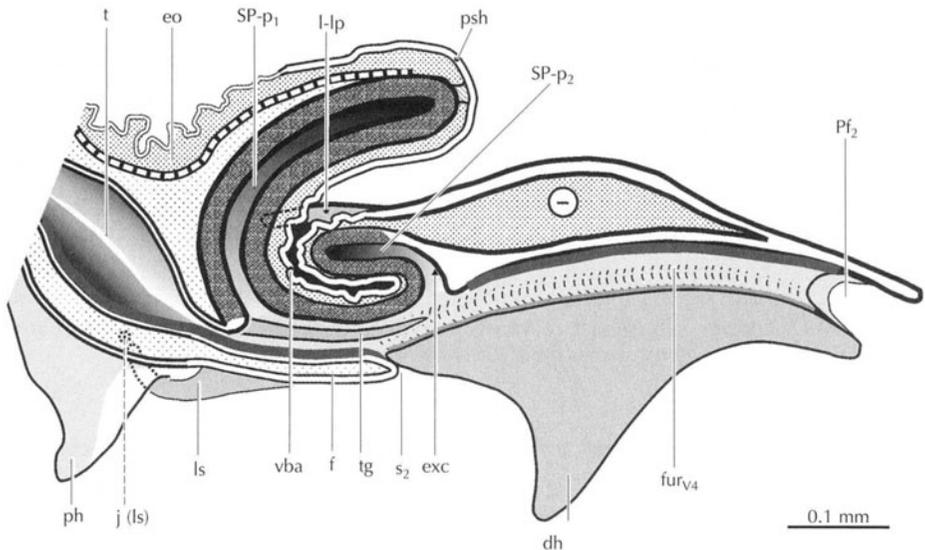


Figure 19: *Choristhemis flavoterminata* — slightly parasagittal section (cf. the lateral aspect of the tongue 'tg') through the decompressed glans. A median septum, which divides the V4-lumen (ventral to the V4-furrow), is not shown. The V4 has been elevated to show details of its ventro-basal region. Abbreviations see p. 262.

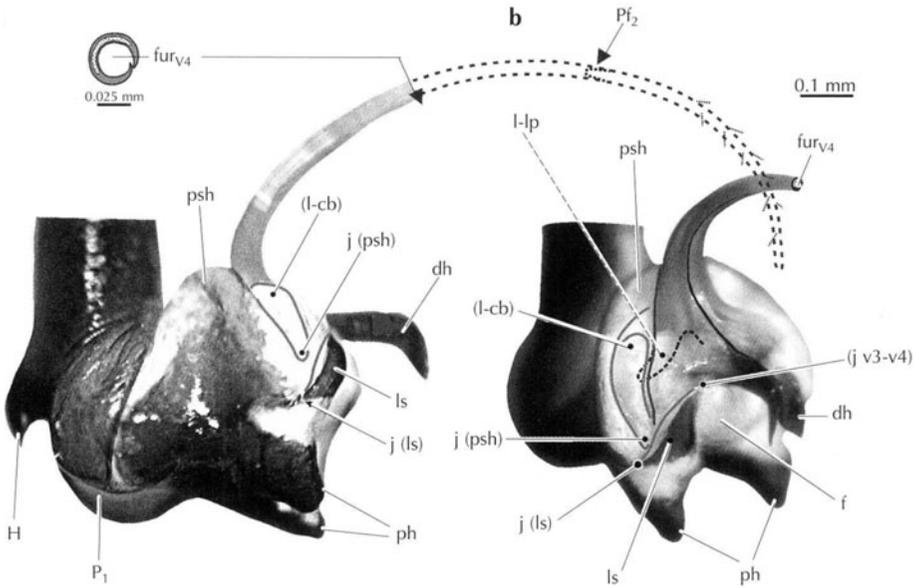


Figure 20: *Eusynthemis nigra*, part of V2, V3 and decompressed glans — shown in (a) oblique lateral and (b) oblique distal view; the long V4-furrow is cut.

A transverse hinge-joint axis, running through the joints 'j (ls)' of both sides, apparently functions as the essential axis for the lifting (during compression) and lowering (during decompression) of the V4. The dorsal movement of the V4 expands on both sides a ventro-lateral membranous region between V3 and V4, which has been designated the 'lateral collapsible box' (l-cb). Each lateral collapsible box is linked dorsally with the dorso-lateral region of the proximal shelter 'psh' via a joint 'j (psh)' (for these structures, which are not illustrated for *C. flavo-terminata*, cf. Fig. 20 and below).

The movements of the V4 include the processes 'f' and the lateral sclerites. Since the medial parts of the lateral sclerites are situated dorsal to the movement-axis, the proximal horns are indented at their base during the V4-lifting.

The proximal pouch of the SP-pump cavity (SP-p₁) is large, but the distal pouch (SP-p₂) is small, producing a strongly asymmetric aspect in the longitudinal section; for comparison see the more symmetric pouches of Gomphomacromiidae and 'Corduliidae' (Figs 22b, 23a). The SP-p₁ is placed inside a large protruding 'collar' of the distal V3-region, which corresponds to the proximal shelter 'psh' of *O. cancellatum*. The dorso-proximal region of the SP-p₂ is fitted in a proximal excavation (exc) of the V4-furrow. On account of the orientation of the SP-p₂, its thickly resilin-covered wall forms an S-bend, which merges into the wall of the SP-p₁.

During the dorsal rotation of the V4 + V3-processes 'f' in the compression-phase, two ventro-basal lever-processes of the V4 (l-lp) probably are essential for the enlargement of the SP-pump cavity. The ventro-distal rotation of these processes should mainly dilate the SP-p₁ via a displacement of the lateral cavity-region, since the lever-processes are fused with the lateral corners of the SP-pump wall. Concerning the overall-dilatation of the SP-pump cavity, this displacement is thought to be assisted by a ventral movement of the proximal shelter (psh) and a ventro-distal directed inflation of a ventral balloon (vba), which is situated between the 'l-lp'. It is expected, that the transformation of the two SP-pump pouches – which are very narrow in the resting phase – into one large SP-pump chamber is accompanied by a bistable effect.

Eusynthemis nigra (Tillyard)

E. nigra exhibits a very long bowed V4-'filament' (Fig. 20a). This filament is not homologous with the at first sight similar distal filament (d-fil, Figs 17, 18) of *O. cancellatum*. Instead – exhibiting a distinct furrow (with a very small diameter), into which proximally the orifices of the pouches of the SP-pump open – it is homologous with the V4-furrow as a whole. This long filament represents a functional 'tube', since it is practically closed through the overlapping border of the left side rim of the furrow (Fig. 20, cross-sections). The V4 of *E. nigra* can be characterized as a long 'injection syringe' for sperm.

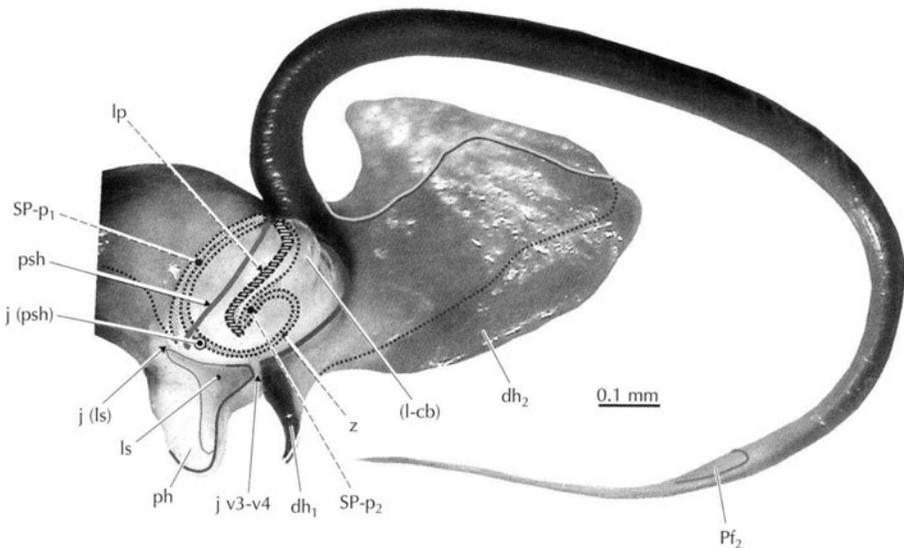


Figure 21: *Synthemis serendipita* — distal V3 and decompressed glans in lateral view. Indication line 'psh' points to the lateral rim of the proximal shelter, which has been re-touched; indication line 'z' indicates the wall of the SP-pump bottom between SP-p₁ and SP-p₂ (tongue omitted); lp: fused lateral lever-processes. Further abbreviations see p. 262.

Synthemis serendipita Winstanley

This large synthemistid species corresponds to *E. nigra* with respect to its very long V4-furrow (Fig. 21). The distal horns of the rims of the furrow however are bipartitioned (dh_1 , dh_2); the dh_2 consists of a large lamella, which is very unequal on the left and right side (investigated specimen only?).

S. serendipita apparently acquired an especially wide range of V4-mobility. To make this possible, the processes 'f' have been largely reduced and the lateral sclerites 'ls' have been displaced proximally. The movements of the V4 now include the proximal horns (ph). The joint 'j v3-v4', which is situated at the distal end of the lateral sclerite, apparently gained in importance in this species; instead it is estimated as of minor importance in *C. flavoterminata* and *E. nigra*, where V4 and processes 'f' (including 'ls') are lifted and lowered as a unit (for 'j v3-v4' of *E. nigra* cf. Fig. 20b). Since the V4 of *S. serendipita* can also bend in a flexible region in between the distal horns dh_1 and dh_2 , three joints (joint-like regions, respectively) are arranged in a series, to allow an extensive V4-movement; 'j (ls)' and 'j (psh)', which lie near to one another, have been simplified to a single joint in this consideration.

The lateral lever-processes (l-lp) are fused to a single long sclerite (lp); the rotation of this sclerite during V4-elevation apparently influences the whole internal region of the proximal shelter, with inclusion of the SP-p₂ apex, which is attached to it.

GOMPHOMACROMIIDAE AND CORDULEPHYIDAE

Gomphomacromia paradoxa Brauer

As in *C. flavoterminata* and *E. nigra* (cf. Synthemistidae), the ventral V4 of *G. paradoxa* bifurcates proximally, forming two lever processes 'l-lp' (Fig. 22). These processes, which are bowed dorsally at their ends, are cushioned in the resting-phase beneath the proximal shelter (psh). A dome-shaped sclerite – the vestige of the proximal pump-sclerite 'p-ps' of the 'Corduliidae' (cf. below) – is fitted medially into the cleft between the 'l-lp'.

In contrast to the Libellulidae and Synthemistidae, the SP-pump is represented in the resting-phase by two thin-walled pouches (Fig. 22b); the walls of the SP-pump show a dark pigmentation. The SP-p₂ is smaller and extends on both sides laterally into the process 'l-lp' (line 'y' in Fig. 22b), where it is attached. The SP-p₁ is attached on its lateral sides to the lateral collapsible boxes (l-cb, Fig. 22a), distal of the joint 'j (psh)'; medially it is fused with the membranous region ventral to the sclerite 'p-ps' via a connecting structure (con).

The lateral region between V3 and V4 is complicated. Its proximal part is represented by the joint-region 'j (psh)', which is situated between the lateral collapsible box ('l-cb') and the dorsal region of the proximal shelter 'psh' (Fig. 22a). Dorsally 'j (psh)' and 'l-cb' are combined with the V4 via an elastic ligament (li).

Experiments indicate that the whole region is essential during compression: both end-parts of the ligament apparently function like joints, whereas the part in between will be stretched. Accordingly the whole lateral membranous region between V3 and V4 allows an extensive dorso-distal movement of the V4 during compression, enabling the V4-base to leave the proximal shelter. Resulting from this movement, the extended bowed bottom-membrane of the SP-pump (Fig. 22b: between SP-p₁ and SP-p₂) will be stretched. Since the SP-pump bottom is at the same time evaginated together with the inflating and evaginating ventral balloon (vba),

the hitherto concealed ventral parts between V4 and V3 will form a large protruding bubble in the compressed condition of the vesica spermalis. This protrusion consists externally of the ventral balloon + sclerite '(p-ps)', with inclusion of the surrounding membrane; internally it consists of the now expanded (and thus single-chambered) large SP-pump cavity.

The play of dorsal movement of the V4 is extensive. This is made possible by the special organization of the dorso-apical V3: (1) the lateral sclerites of the processes 'f' are bendable in a proximal flexible zone 'flz(ls)'; (2) these flexible zones co-operate with the joints 'j v3-v4', situated between the lateral sclerites (ls) and the V4; (3) the proximal horns (ph) are bendable upwards in proximal flexible zones 'flz(ph)', in spite of their dorso-ventral thickness. Accordingly in all flexible zones elastic energy will be stored during the lifting of the V4, which will be added to the elasticity stored in the ligament 'li' between 'j (psh)' and V4. During decompression these elastic 'springs' will cause a quick lowering of the V4, which accompanies the ejaculation of the sperm via the Pf₂.

Similar to the Synthemistidae, in *G. paradoxa* the processes 'f' are fused except for the tip. However, since the proximal horns (ph) are depressed, the processes 'f' are concealed in their mid-region. The slit between the two proximal horns is extended proximally and is deeply invaginated and excavated laterally, forming the grooves 'gr' (Fig. 22b). The function of these cavities is unclear.

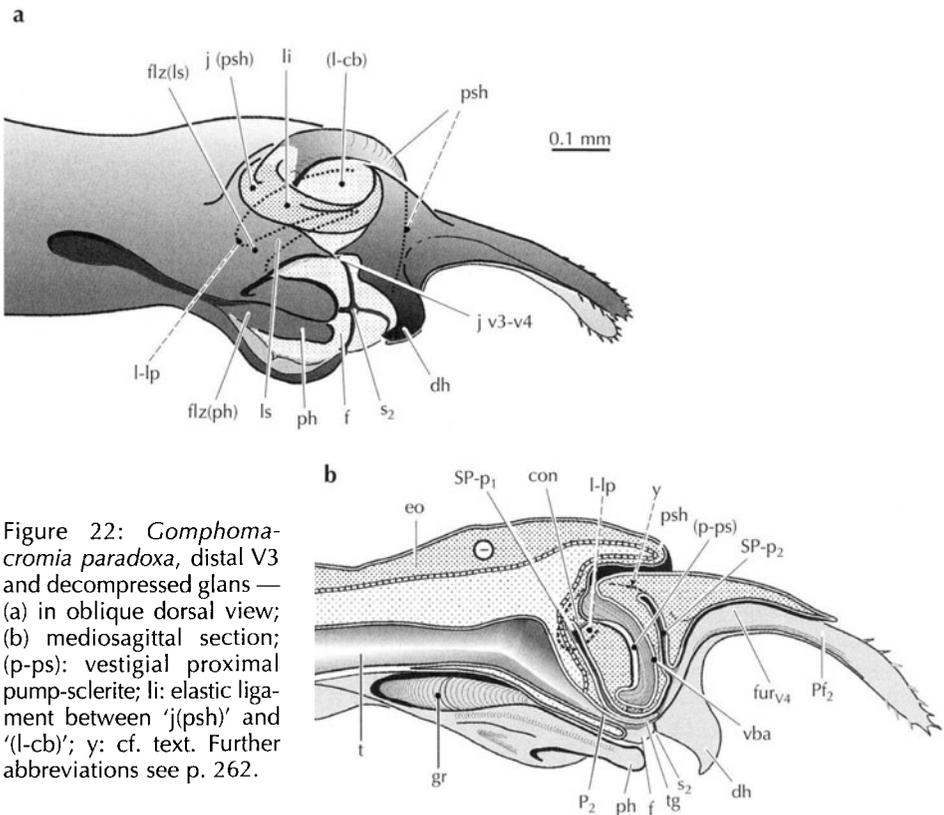


Figure 22: *Gomphomacromia paradoxa*, distal V3 and decompressed glans — (a) in oblique dorsal view; (b) mediasagittal section; (p-ps): vestigial proximal pump-sclerite; li: elastic ligament between 'j(psh)' and '(l-cb)'; y: cf. text. Further abbreviations see p. 262.

Cordulephya pygmaea Selys and *C. bidens* Sjöstedt

Only the glans of a single immature male of each of these species (not illustrated here) was available.

Briefly summarized, *C. pygmaea* and *C. bidens* are similar to *G. paradoxa* with respect to the (less distinct) grooves along the medial sides of the depressed proximal horns and to the structure and proportions of the SP-pump pouches. The proximal pump sclerite '(p-ps)' is also present as an isolated sclerite in these species, but, in contrast to *G. paradoxa*, it is not domed.

The lateral lever processes (l-lp, cf. *G. paradoxa*) are lacking (or fused with one another?). The proximal horns are large, totally concealing the shorter processes 'f'. Since this character was found very similar in the 'corduliid' *Oxygastra curtisii* (Dale), the glans of the Cordulephyidae is evaluated as transitional (cf. Fig. 26 and chapter 'Evolution of the glans').

'CORDULIIDAE'

Somatochlora metallica (Vander Linden)

In the resting-position of the V4 (= decompressed state, Fig. 23a), the sperm-pump cavity of *S. metallica* is compressed to two narrow, approximately equal large pouches SP-p₁ and SP-p₂, situated between the distal orifice of the V3-tube and the beginning of the V4-furrow. The wall of these pouches is thin and contains resilin.

As in the previously treated groups of the Libelluloidea with two SP-pump pouches, the compression of the vesica spermalis (Fig. 23b) expands the pouches into one large sperm-pump chamber (SP-p). In this case, however, this is mainly due to a downward rotation of a ventral sclerite of the V3, the proximal pump-sclerite (p-ps), which articulates latero-proximally with the ventral edges of the V3 via the joints 'j (p-ps)' (Fig. 24c). The joints of both sides define a transverse hinge-joint axis, which is indicated in Figure 23a (ax).

At the proximal edge of the ventral surface of the V4-furrow a membranous cushion 'mc' (obviously representing resilin) is developed, which was found especially conspicuous in *S. flavomaculata* (Vander Linden). During the ventral rotation of the proximal pump-sclerite, this region may function as a temporary stop for the tip of the sclerite, which will be abruptly released, causing a bistable effect during the spreading of the SP-pump cavity – similar to the snapping-effect of fingers.

The enlargement of the SP-pump-cavity during compression (Fig. 23a-b) is accompanied and supported by the 'normal' dorsal movement of the V4. A bottom-sclerite of the V4 (bo) is rotated during this movement dorso-distally, carrying along the wall of the SP-p₂, which is connected to it via a connecting structure (con). The wall between the two pouches is carried ventro-proximally by the proximal pump-sclerite, which is connected to it at its tip. As a result, the proximal and distal parts of the wall of the SP-pump are moved in different directions.

The SP-pump cavity is also expanded laterally during compression: its lateral regions, which resemble collapsible boxes (cf. 'l-cb' in Figs 24a, 24b for *Cordulia aenea*), are unfolded. This effect is due to the p-ps-movement as well as to the inflation of the ventral balloon (vba).

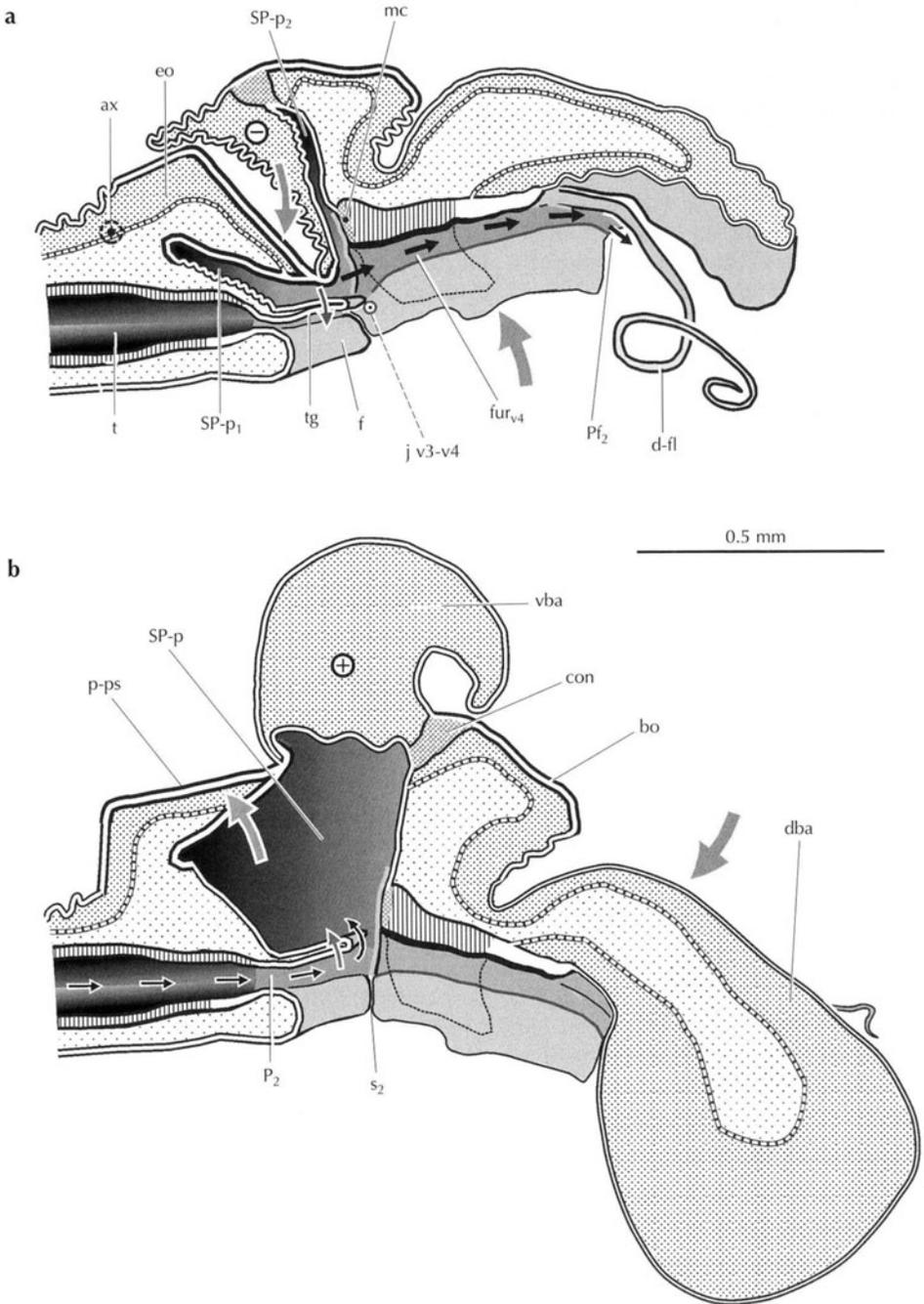


Figure 23: *Somatochlora metallica*, mediosagittal sections through distal V3 and glans — (a) decompressed glans; (b) compressed glans. Sperm-flow and movements of V4, proximal pump-sclerite (p-ps) and tongue (tg) indicated by black and differently grey arrows; ax: hinge joint axis of the p-ps-movement, running through the j (p-ps) (cf. Fig. 24c) of both sides; mc: membranous cushion; further abbreviations see p. 262.

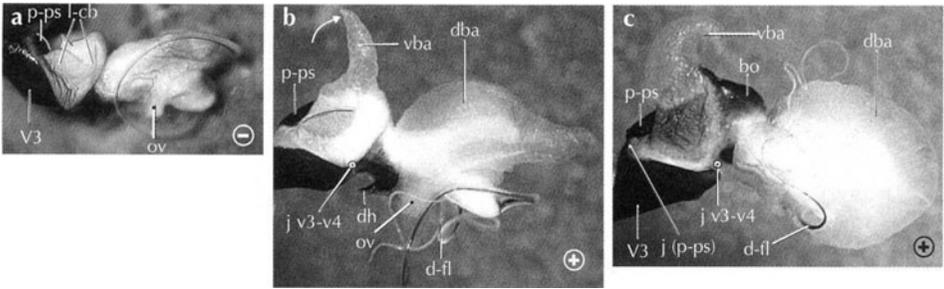


Figure 24: Distal V3 and glans in lateral view of — (a, b) *Cordulia aenea*, and (c) *Somatochlora metallica*. The glans is inflated in (b) and (c); white arrow in (b) indicates the movement of the membranous apex of the ventral balloon. Abbreviations see p. 262.

The distal orifice (P_2) of the V3-tube is widened and the tongue (tg) is lowered (dark grey arrow in Fig. 23b), partly because of the ventral movement and pull of the proximal pump-sclerite, partly passively on account of the sperm-flow and the SP-pump suction. The ventral movement of the tongue clears the way for the inflow of sperm into the SP-pump cavity. At first, for a short distance, the sperm should flow along the dorsal surface of the tongue; this explains the presence of a longitudinal dorsal furrow on the tongue (not indicated in the Figs). It is assumed that sperm, which is pressed distally out of the reservoir, is accelerated by the suction of the quickly expanding SP-pump cavity and that the SP-pump is immediately filled with sperm.

The compression of the erectile organ inflates two large soft-skinned regions of the glans, at first the ventral balloon (vba) and then the distal balloon (dba). The inflating distal balloon seems to overlap the functional pores (Pf_2 , cf. below) and to close them.

Two distal flagella (d-fl), inserted on both sides near the end of the V4-furrow, are twirled strongly and erratically during compression. These movements involve mainly the left side flagellum, which is much larger, showing a thick resilin-packed base. The strong movements of this left side flagellum were observed to begin later than the movements of the right side 'd-fl'.

During the decompression (Fig. 23b-a) the effects described above were reversed. Whereas the balloons deflate relative slowly, the proximal pump-sclerite quickly snaps dorsally into the SP-pump cavity, accompanied by a ventro-basal rotation of the V4-bottom (bo) together with the attached distal SP-pump wall. These movements are obviously accelerated by elastic effects of the pump walls (which contain resilin) and external walls and joints, which have been stretched in the compression-phase. The distal orifice of the V3-tube (P_2) is now narrowed (perhaps even completely closed). The broad tongue, which is pushed dorsally (to some extent passively by the expelled sperm), accessorially closes the P_2 with its proximal region; it also overlaps the dorsal cleft between the V3 and V4 and improves its tightness.

Since the V4-furrow bifurcates distally, there are two distal furrows and functional pores 'Pf₂'. The larger right side pore is situated more proximally at the base of the (smaller) distal flagellum (d-fl) of this side. The smaller functional pore of the left side instead is situated more distally, at the base of the large left side flagellum, which is inserted more distally. The sperm of the collapsing SP-pump cavity is expelled out of the V4-furrow latero-dorso-distally, presumably using both functional pores. This double-jet ejaculation might represent a mean to directly charge the two receptaculi seminis of the female.

In both the compression and the decompression phase the dorsal cleft between the V3 and V4 has been found sealed by the close contact between the cushion-like walls of the processes 'f' and the softly sclerotized dorsal V4-base. The ventral movement of the V4 during decompression consists, therefore, not only of rotation around a stable axis, running through the joint-pivots j v3-v4 of both sides, but, superimposed on this rotation, of an elastic deformation of the V4: the V4 appears to be elastically 'compressed' in the ventro-proximal direction; the V3/V4-cleft is kept closed by this and the closure of the distal V3-porus P₂ is supported.

Cordulia aenea (Linnaeus)

C. aenea (Figs 24a, 24b) is similar in fundamental features, but is different with respect to the form of the ventral balloon and the more asymmetric construction of the V4. In this species the distal part of the oblique V4-furrow is overlapped by an inflating dorsal part of the distal balloon (ov, Fig. 24b), which is apparently vestigial in *S. metallica*. This part extends in *C. aenea* to the right side, forming a distinct lobe that conceals the base of the right-side distal flagellum and the Pf₂. Only the left-side rim of the V4-furrow is equipped with a hooklike distal horn (dh).

The vesicae spermalis of further species – *Macromia splendens* (Pictet), *Oxygastra curtisii* and *Pseudocordulia elliptica* Tillyard – were investigated for comparison and also classified as fundamentally primitive-'corduloid' (cf. Evolution of the glans).

EVOLUTION OF THE GLANS

Evolution of the 'two-way tap'

The attempt to trace back the evolution of the different types of glans of the Anisoptera encounters difficulties. The main problem for reconstruction is the fact that the extant types of glans appear to have already evolved complicating differences.

At first it will be necessary to investigate the question of the origin of the distal segment V4 of the vesica spermalis in the stem group of the Anisoptera. There are two possibilities:

- A segmentation of the V3 by installation of a hinge inside this segment. This possibility would imply that the distal orifice of the (former) V3 would have continued to function as an ejaculation-orifice in the V4 (Pf₂); the Pf₁ would represent a new (= secondary) orifice.

- The additional formation of a ventro-distal outgrowth of the V3 as a two-lobed inflatable structure, which in a later state formed a furrow, prolonging the V3-furrow. In this case the Pf₁ would have continued to function as the primary pore of ejaculation. Later this pore could have been restricted functionally and brought into action only temporarily, whereas a Pf₂ of the V4 could have become involved more and more. Accordingly the Pf₂ would represent a secondary orifice of sperm-transfer.

The first possibility is favoured on account of the fact that the V4-furrow appears as a simple continuation of the V3-furrow in many Aeshnidae, as also of the possibility of a more direct derivation. It will be alone investigated here in detail.

The anisopteran vesica spermalis evolved from the simple one-segmented zygoteroid organ by prolongation of its ventro-distal part, including the orifice of the reservoir (Pfau 1971). During this process, the successively elongated orifice, which formed a furrow, was closed to a functional 'tube' by an approach of its dorsal rims – except for the region of the filling-pore P₁, which remained membranous, functioning as a valve and only opened (from the outside) when the reservoir is filled. A short distal part of the furrow was left also 'unclosed' as a slit-like primary ejaculation-'pore'. This elongation and differentiation of the vesica spermalis was accompanied by a ventro-caudad bowing and a division by joints into three members.

Then, by evolution of a further articulation (j v3-v4) in the proximal region of the distal 'slit-pore', a possibility to move the tip of the vesica spermalis was evolved. This segmentation of the V3, into V3 and V4, necessitated as well the formation of membranous regions in the wall of the sperm-furrow as in the external wall. On a level with the new articulation a further pore of ejaculation (Pf₁) could easily evolve; the primary distal 'slit-pore' became divided by this into two 'pores'. The proximal orifice Pf₁ could only function as a separate ejaculation orifice, when the V4 was lowered. At this state the tongue may have separated dorsal and ventral sperm-jets to a certain extent.

The V4 attained a further function: it became inflatable to anchor the vesica spermalis inside the female vagina; for the necessity of evolution of the erectile organ cf. Preliminary remarks.

The evolution of a movable V4 can be interpreted as the establishment of a possibility to produce sperm-jets of different directions. Caused by active (hydraulic) and passive (inflation- or ligula-effects) movements of the V4, a dorsal jet of sperm (Pf₁) could have been supplemented by a sperm-scattering jet, which used the rotating V4-furrow and Pf₂.

Presumably the ancient 'slit-pore' remained at first in a rather undifferentiated furrow-condition and was specialized later (probably by multiple convergent pathways) into a more concrete Pf₂. This assumption is founded on the fact that improvements of the dorsal seal of the V4-furrow are attained differently in the extant groups.

The early V4 is designated here as the 'pre-gomphaeschnoid' glans, since especially the derivation of the glans of the Gomphaeschnidae (two-way tap with tongue) affords only small alterations.

In the Gomphaeschnidae a strongly downwardly-bent resting position of the V4 in combination with a small range of mobility (which apparently ensure a suffi-

ciently retrograde directed Pf_2 -jet of sperm during the second half of the compression) and a special function of the tongue inside a narrow 'Pf₁-channel' had been evolved. In *Gomphaeschna furcillata* the tongue is very short with respect to its freely protruding distal part. This prevents a turn-over into the V4-furrow, guaranteeing the function as a secure seal during the first part of compression.

The presence of a tongue in the Gomphaeschnidae and all other groups of Anisoptera, with exception of the Aeshnidae, indicates its secondary reduction in the Aeshnidae; the tongue was substituted in the Aeshnidae by the special seal 's₁'.

The procedure of sperm-discharge in the Gomphaeschnidae and Aeshnidae appears at first glance as a curiosity: the obliquely orientated or bowed V4-furrow, which is involved only during the second part of the elevation of the V4, expels the sperm ventro-proximally, in retrograde direction; this direction however contradicts the direction of the correlated elevation-movement of the V4-furrow. The 'two-way tap' apparently indicates a compromise, suggesting an autapomorphic nature. This compromise implies the capability to produce a pure Pf₁-jet of sperm at the beginning of the compression – which depended at first on the tongue as the necessary seal-structure and later, in the Aeshnidae, on the 's₁' – and to add a pure Pf₂-jet with a different direction in the second part of compression. Pure jets will be especially strong and may be advantageous as well for a direct loading of the bursa copulatrix as for a sperm displacement. On account of the peculiar solution of the Aeshnidae, this group is considered here as monophyletic. The primitive glans of the Gomphaeschnidae, on the other hand, may represent either the glans of the stem-species of a group 'Gomphaeschnidae + Aeshnidae' or may have existed already at the base of the Anisoptera.

The Gomphaeschnidae and Aeshnidae show characters, which are evaluated as primitive: a V3-furrow (in most genera) and the absence of a distal sperm-pump. The possibility exists that the gomphaeschnoid glans (two-way tap with tongue) could have represented the starting point for groups which evolved a sperm-pump. At first sight, however, this implies difficulties in the case of the PS-pump evolution. These difficulties originate from special characters of the 'two-way tap'. The fact that the V4-furrow would be 'pinched off' by the tongue during decompression (cf. Fig. 5), seems to contradict a derivation directly from the gomphaeschnoid type of glans: instead of successively being widened, an emerging PS-pump would be 'sucked' to its own seal during decompression, and the filling of a (initially small) PS-pump cavity would be stopped abruptly. A reduction of the tight sealing by the tongue in the decompression phase would be necessary. This, however, requires only minor alterations. Therefore the question, whether the 'PS-pump' derived from a 'pre-gomphaeschnoid' glans (cf. above) or from a 'two-way tap with tongue' (gomphaeschnoid type) is open.

Evolution of the pressure-suction pump

The morphologic place of origin of the PS-pump is already detectable in the Aeshnidae and Gomphaeschnidae ('c', Figs 2a, 3a, 5); this membraneous region is part of the V3/V4-joint, delivering the necessary play of movement of the V4-furrow. The initially small pocket has been enlarged during evolution into a cavity, which began to be widened synchronously with the decompression of the V4, and was squeezed synchronously with the compression. A special requirement for its func-

tion must soon have become important: during the decompression, a stable, not deflating section of the external cuticula is afforded, to make room for a widening of the PS-pump cavity. In the Austropetaliidae this cavity is already very conspicuous as a curious ventral swelling of the V3, which is protected by the ventrally rotated V4 in the resting position (Fig. 13b). Since this external region of the PS-pump has soon been integrated into the glans, it appears in all other groups as being part of the V4.

The total absence of a vestibule in the Austropetaliidae appears to be a primitive feature. On the other hand, several features correspond to a state of glans, which can easily be positioned between a pre-gomphaeschnoid (or gomphaeschnoid) glans and the more advanced glans-types with PS-pumps: (1) the rather small PS-pump, (2) the dorsal movement of the V4-furrow during compression, leading to a connection between the V3- and V4-furrow, (3) the co-ordinated closing of the Pf_1 at the seal-point s_2 and (4) the function of the short tongue as a separating lamella, and accessorially as a non-return valve of the V3-furrow and reservoir. Other features, as e.g. the very large scope of movement of the V4 in its much elongated ventral joint region, represent autapomorphic characters of the Austropetaliidae.

At this stage of evolution, the main advantage of a vesica spermalis equipped with a PS-pump, was, compared to the pre-gomphaeschnoid and gomphaeschnoid glans, the participation of the decompression-phase in the emptying of the sperm-reservoir. Since during each decompression sperm was sucked distally into the PS-pump and was then expelled in the compression phase, a distal auxiliary pump had been evolved that supported the simple pumping-mechanism of the V1. This assistance probably was important, especially in the prolonged vesica spermalis of the Anisoptera, since the reservoir is not equipped with an own musculature.

A vestibule was then evolved at the end of the V3-tube, dorsally of the PS-pump. The early dorsal jet of sperm via the Pf_1 automatically lost importance. As this vestibule got larger, increasing amounts of sperm were kept back during compression in its cavity and placed at the disposal of the sucking PS-pump in the decompression-phase; this sperm of the foregoing compression-phase was then expelled via the V4-furrow and Pf_2 during the next compression. In principle the sperm-transfer had become 'three-phased'.

This type of a primitive three-phase sperm transmission is already present at the level of the Gomphidae. However, a primitive 'austropetalioid' feature seems to have survived in this group: the V3- and V4-ducts are still directly connected, although they presumably work as a direct passage only during the very first compression. This means that the V3-sperm jet – in spite of partly being accumulated inside the vestibule – will be mixed with the sperm from the PS-pump: in the Gomphidae the different sperm-streams, ejected from the PS-pump and reservoir + vestibule, are not yet completely separated. Since the jet of sperm expelled from the PS-pump is evaluated as superior, the tongue should function just as in the Austropetaliidae, as a non-return valve of the V3-tube (+ vestibule in this case).

During the further evolution, the direct connection between V4-furrow and V3-tube has been abandoned by development of a level-difference between the ducts: The V4-furrow was translocated ventrally and was in that way exclusively connected with the PS-pump. The tongue, which automatically approached the dorsal rim of the V4-furrow, became involved in the formation of a new seal, together with

the proximal rims 'c-ts' of the V4-furrow. The former seal 's₂' was abandoned, as the level-difference grew; it was replaced by the new seal 's₂*'. A series of further structural differentiations (col, tr, l-gr; cf. Figs 6-11 and text) led to an apparatus in which the sperm-transmission is divided into three phases but nevertheless is ensured by conducting and sealing devices that work on account of the V4-movements during decompression and compression.

The translocation of the V4-furrow automatically implicates the possibility of a dorso-ventral enlargement of the PS-pump during evolution. By contrast, in some Gomphidae, e.g. *Ictinogomphus ferox* (Rambur), the PS-pump has been enlarged much in the longitudinal direction.

At the base of the Petaluridae + Chlorogomphidae + Neopetaliidae + Cordulegastridae (Fig. 26) the common constructional platform for the 'advanced three-phase sperm-transfer' was reached. The persistence of ancient characters, e.g. the Pf₁ in the Chlorogomphidae, however indicates that certain alterations occurred convergently and that different levels of organization have been attained in the extant groups. In the Cordulegastridae e.g. the Pf₁ has been reduced and the horns of the processes 'f' have apparently moved together, to form – in combination with the small original vestibule – a relative large, but poorly defined vestibule (cf. Figs 7, 8).

A common feature of the 'advanced three-phase sperm-transfer' is that sperm, ejected from the V3-tube during compression, is deposited to a large extent inside a more or less large vestibule and/or externally between the (enlarged) processes 'f'. The sperm will be automatically accumulated at these places, especially at the end of the compression, when the stream slows down. In this 'first phase' of sperm-transfer there is (in contrast to the Gomphidae) no direct connection between the vestibule and the V4-furrow. In the 'second phase', during the following decompression, the sperm of the vestibule (and external sperm between the horns 'h-f') will be 'confiscated' by the sucking PS-pump – together with some new sperm from the V3-tube and reservoir, which has been sucked distally – since the vestibule-PS-pump passage is now open. In the 'third phase', the next compression-phase, a pure PS-pump jet of sperm is expelled via the Pf₂.

The main advantage of this type of PS-pump is supposed to lie again in the possibility to produce pure jets of sperm, which should be, in the absence of interference with sperm from the reservoir and vestibule, of relatively high velocity. Only in the case of the PS-pump (and not in the case of the SP-pump) such a curious solution seems to have been necessary to fulfil this purpose.

The Chlorogomphidae indicate that the orifice Pf₁ was presumably used as a functional pore for a long time – at least to fill the 'external vestibule' between the horns of the processes 'f'. This would correspond to the presumption, that various streams of sperm were expelled at the same time in an earlier evolutionary state during the compression-phase (as in the Austropetaliidae): a dorsal stream through the Pf₁, accompanied (in the elevating V4) by a ventral stream through the V4-furrow and Pf₂, which was strengthened by sperm from the PS-pump. These different jets of sperm could have performed different functions: whereas the Pf₁-jet could have directly 'loaded' the bursa copulatrix of the female, the Pf₂-stream could have participated in this, but could at first have produced a retrograde flow, since the V4-furrow is involved already in the lowered V4 (in contrast to the gomphaeschnoid and aeshnoid glans).

These considerations throw further light on the principal advantages of the PS-pump. As already mentioned, the ancient mechanism of compression of the sperm reservoir seems to represent a critical factor in the prolonged vesica spermalis of the Anisoptera. The newly evolved PS-pump constitutes a distal organ, which is directly connected to the amplifier of the pressure forces 'erectile organ' (cf. Preliminary remarks). Therefore PS-pump jets of sperm should be stronger than jets merely produced by compression of the reservoir. According to this, the advantage of a de-coupling of the V3-tube from the PS-pump + V4-furrow would lie in the possibility of producing pure Pf₂-jets of sperm, which are amplified. This could be of value in sperm-removal actions, especially when abilities exist to produce jets of different direction – e.g. as diverted parts of the Pf₂-jet (cf. Fig. 7b).

Summing up, several correspondences in finer details between the Petaluridae, Chlorogomphidae, Neopetaliidae and Cordulegastridae substantiate a monophyletic evolution (Fig. 26). The Gomphidae, which are interpreted as transitional with respect to the three-phase sperm-transfer, are the most basal taxon in which the vestibule is present. This group presumably derived from a stem-species with an (early) austropetaliod glans. The Austropetaliidae, in their turn, correspond in the possession of the PS-pump, which is considered as an 'unique invention'. The comparative investigations indicate a successive, additive evolution of constructional and functional features, which corroborates a monophyletic group 'Petaluroidea' (Pfau 1991).

Evolution of the suction-pressure pump

The mechanism and function of the SP-pump of the Libelluloidea is totally different. First: it is contrary in its co-ordination with the compression-decompression rhythm (Fig. 25). Second: it is also much different in its functional prerequisites at the beginning of the evolution. Whereas the PS-pump requires a relatively rigid section of the ventro-apical V3-region in order to expand independently during decompression, the SP-pump needs a coupling between the wall of the SP-pump and inflating external parts during compression; in the decompression-phase the SP-pump collapses together with the deflating external structures.

Again a pre-gomphaeschnoid or gomphaeschnoid glans – equipped with a tongue, i.e. without the aeshnoid seal 's₁' – is close at hand to have represented the starting point of evolution. Although functioning as a valve in different phases (compression and decompression, respectively), there are indications that the tongue is homologous in the groups with PS- and SP-pumps: *Cordulia aenea* e.g. shows a pair of supporting cuticular rods inside the tongue, which broaden and diverge proximally, in principle corresponding to the conditions found in the Cordulegastridae and Gomphidae. At the beginning of the SP-pump evolution, the tongue could have functioned just as in the pre-gomphaeschnoid (or gomphaeschnoid) glans: as a device to separate a Pf₁-stream of sperm in the early compression-phase. Later it should have become useful to close the P₂ as a non-return valve in the decompression-phase, and also to improve the sealing of the dorsal V3/V4-cleft.

During the early SP-pump evolution only parts of the whole sperm volume presumably branched off from the main-stream to flow into the pump cavity. Initially this should have happened in the late compression phase, when the sperm stream,

which enters the V4-furrow, gets slower. As the SP-pump cavity enlarged, this temporary 'confiscation' of sperm became more important. The Pf_1 lost its function (convergently to the Petaluroidea) by a persistent sealing of the cleft between the dorso-proximal border of the V4-furrow and the processes 'f' (s_2 , Fig. 23b), and the sperm was aspirated only from the stream that entered the V4-furrow and left it through Pf_2 . The collapse of the SP-pump cavity in the decompression-phase led at first only to a continuation of the Pf_2 -stream of the foregoing compression, producing a second peak of sperm amount and velocity. Then the Pf_2 lost its function in the compression-phase and the sperm was expelled through it only during decompression.

The suction-effect of the SP-pump was apparently successively improved during evolution. An essential requirement was the early and then persistent sealing of the Pf_1 ($-s_2$), which should have automatically improved the suction. A later step was the sealing of the V4-furrow and Pf_2 by means of an inflation of the tongue during compression (cf. Libellulidae), extending the function of the tongue as a gasket to the compression-phase. It was not possible to check whether this also applies to the Synthemistidae, but the tongue seems not to be long enough in this group to perform a similar function.

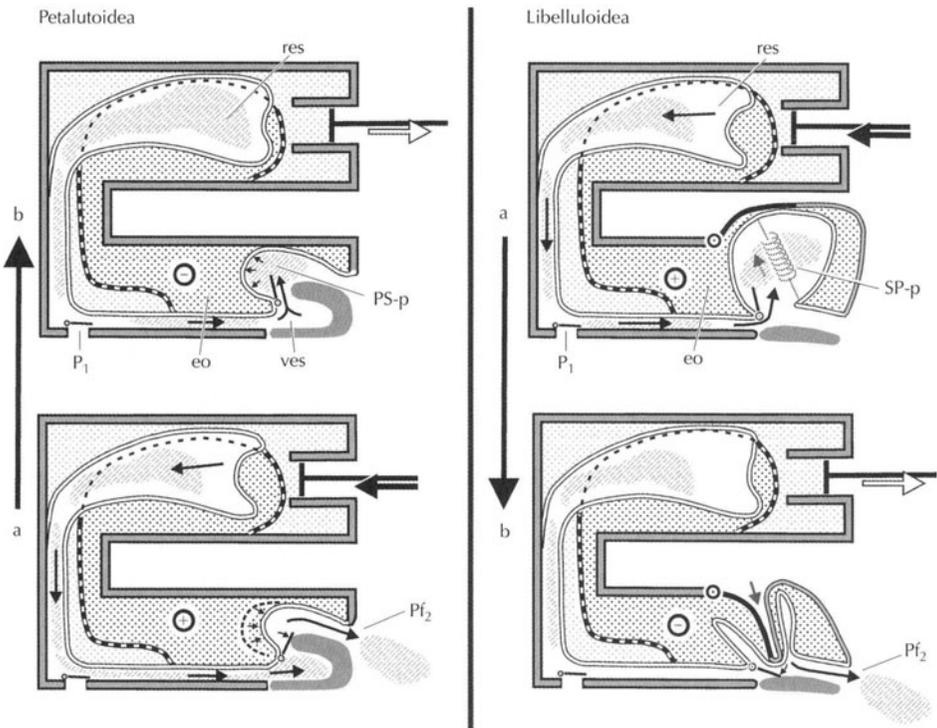


Figure 25: Principal functions of the different sperm-pumps of the Anisoptera, approximated in certain details (valves, piston) to technical apparatus — (a) Petaluroidea, type with three-phase sperm transfer; (b) Libelluloidea, primitive corduloid type; res: sperm reservoir; further abbreviations see p. 262.

A successive improvement of the function of SP-pumps is indicated by the distribution of certain characters in different groups of the Libelluloidea, presumably reflecting the succession of phylogenetic ramifications:

The series 'Corduliidae'-Cordulephyidae-Gomphomacromiidae-Synthemistidae-Libellulidae (Fig. 26) demonstrates step by step an advancement of complexity and functional perfection (additive typogenesis), indicating the direction of evolution. The primitive corduloid glans shows a rather simple lever-guided glans inflation, which leads to an extension of an approximately symmetrically folded, thin-skinned SP-pump from two sides. During this extension, the lateral regions of the pump-cavity, in combination with the external cuticula, behave like unfolding collapsible boxes (l-cb, Fig. 24) on account of three effects of the compressed erectile organ: (1) the ventral rotation of the proximal pump-sclerite (p-ps); (2) the inflation of the ventral balloon, which unfolds mainly the mid-region of the 'l-cb'; and (3) the 'normal' dorsal movement of the V4.

An essential element of the primitive corduloid glans-mechanism, the proximal pump-sclerite (p-ps), was then reduced. In the stem-group of the Cordulephyidae + Gomphomacromiidae + Synthemistidae + Libellulidae the V4-movement and the ventral balloon-inflation presumably acquired more and more importance at the expense of the proximal pump-sclerite: The bottom-sclerite (bo) was prolonged proximally (l-lp) and the importance of the ventral balloon was strengthened. The proximal pump-sclerite, which lost its joints, was vaulted by the formation of the proximal shelter (psh), and became an unimportant sclerite in the membrane of the inner (= dorsal) surface of this outgrowth (cf. Cordulephyidae, Gomphomacromiidae). Proximally the lateral collapsible box was tied via a joint 'j (psh)' onto the latero-dorsal region of the proximal shelter. Now the lateral collapsible boxes of both sides were expanded mainly by inflation of the ventral balloon, which has been enlarged by the addition of the region of the proximal pump-sclerite; the ventral balloon is now inflated in the ventro-distal direction, clearing the way by pushing the V4 dorsally and supporting its 'normal' dorsal rotation.

The formation of a well-defined pivot 'j (psh)' of the lateral collapsible boxes + V4 and the reduction of the function of the proximal pump-sclerite imply a distal shifting of the sperm-pump 'motor'. The function of the proximal shelter is to protect the ventral balloon + V4-base in the resting phase as well as to guide the evaginating parts, including the evaginating sperm-pump bottom.

The Cordulephyidae and Gomphomacromiidae exhibit interesting transitional characters between the 'Corduliidae' and the Synthemistidae + Libellulidae: the sclerite 'p-ps' has already lost its latero-proximal joints and accordingly its former function; the remaining p-ps-vestige is moved ventro-distally as a whole during the compression, and is at the same time rotated ventrally in relation to the SP-p₁ (to which it is attached proximally), in principle recapitulating its ancient corduloid movement.

On the other hand the Cordulephyidae form a transition to certain 'Corduliidae'. *Oxygastra curtisii* for instance corresponds much in the appearance of dorsal structures of the base of the glans, namely in the large depressed proximal horns. Furthermore there are signs of a beginning formation of the proximal shelter (psh) in *O. curtisii* – at the sides of the proximal pump-sclerite.

At the base of the Gomphomacromiidae + Synthemistidae + Libellulidae the large depressed proximal horns presumably had been reduced in size; later, at the base of the Synthemistidae + Libellulidae (?), these smaller horns became erect. In *Gomphomacromia paradoxa* the not yet erected, but already small proximal horns function, together with the enlarged lateral sclerites 'ls' of the processes 'f', as an elastic device, abbreviated in Figure 26 as 'ls-ph spring'. This spring is loaded during the compression (V4-elevation) and accelerates the V4-downward movement and the collapse of the sperm-pump cavity during decompression. Besides this, the movement-range of the V4 is apparently enlarged at this state of evolution, indicating a larger range of sperm-scattering.

It is interesting that medial grooves of the processes 'f' could be found as well in the Cordulephyidae as in the Gomphomacromiidae, presumably a symplesiomorphic feature that was already present in a 'corduloid' ancestor. According to this, these mysterious excavations would have been reduced at the base of the Synthemistidae + Libellulidae.

A further enhancement of SP-pump function was due to the transformation of the SP-pump wall into a thick resilin-layer in the stem-group of the Synthemistidae + Libellulidae. Besides this, the SP-p₂ tended to reduction, the SP-pump pouches becoming strongly unequal. At this state the main 'motor' for the spreading of the pump-cavity was still the ventral balloon.

Apparently the Synthemistidae evolved several autapomorphic features, which can be interpreted as alternative compared with characters of the Libellulidae: In the resting-position the distal pouch of the sperm-pump (SP-p₂) is curved backwards and fitted into the concavity of the large proximal shelter; inside the proximal shelter, the SP-p₁ had been extended far ventro-distally (Fig. 19). This construction affords an extremely large elevation of the V4 to fulfil a total expansion of the sperm-pump cavity, which mainly proceeds in the joints j (psh) and j (ls) (the latter replaced the 'flz(ls)' of the Gomphomacromiidae), which lie near one another. The 'erected' proximal horns (ph) make room for this necessarily large V4-movement. The expansion of the 'curled' PS-pump pouches and the collapse of the SP-pump cavity are presumably accompanied by a bistable mechanism, caused by a temporary distortion of the SP-pump wall.

In contrast to this, the evolution of the libelluloid glans proceeded with a membranization of the medial part of the proximal shelter. This made possible as well the evolution of the proximal balloon (pba) as the establishment of a new source of elasticity to accelerate the pump-cavity collapse: the now separated ventral margins of the V3 (v-mar). The main motor for the spreading of the SP-pump cavity was shifted to this new inflatable proximal region, which functionally replaced the ventral balloon. The spreading and collapsing of the SP-pump is mechanically guided in this type of glans by complex arrangements of suspensory sclerites or appendages. Whether these alterations took place in the stem-group of the Libellulidae or inside the group should be clarified in further studies (for autapomorphic characters of the Libellulidae, concerning the secondary copulatory apparatus, see Pfau 1971: 340).

This reconstruction reveals an extensive evolution of structure and function of the glans in the Libelluloidea, indicating a multiple shifting of the relevant 'motor' for dilatation of the SP-pump and a new formation of elements for its mechanical

guidance. It indicates also successive improvements of elastic aids, concerning the external structures as well as the walls of the SP-pump. It finally led to glans organizations with a complex nesting of structures, which are accordingly difficult to homologize (see e.g. the supposed vestiges of 'p-ps' and 'l-lp' in *Libellula quadrimaculata*), and to apparatus that are capable of producing especially quick sperm-pump collapses and sperm-jets. It is interesting that in the Libelluloidea again the generation of a retrograde stream of sperm seems to be important. This retrograde flow of sperm is attained during the lowering of the V4, i.e. in the second phase of each pumping-cycle, during decompression (Fig. 17a). The same sequence of different directions of sperm-jets is expected in the 'two-way tap' of the Gomphaeschnidae and Aeshnidae – in this case however executed as a whole during the first phase of each cycle, during compression.

Phylogenetic conclusions and evaluations concerning efficiency

The transition from a pre-gomphaeschnoid (or gomphaeschnoid) to a petaluroid glans, equipped with a PS-pump, could be reconstructed step by step. By contrast, there is a large gap at the base of the Libelluloidea: the early constitution of the SP-pump, previous to the 'corduloid' realization, had to be reconstructed without the help of interlinking apparatus. However, although transitional species are presumably not living any more, a hypothetical derivation is possible without constraints, if the pre-gomphaeschnoid or gomphaeschnoid glans is used as a starting point. On the other hand, a derivation of the Libelluloidea from petaluroid ancestors, as would be necessary in the case of the existence of a group 'Cavilabiata', can be excluded, since a transition between PS-pump and SP-pump is unlikely. Such a transition would imply an intermediate state of the glans without a functioning sperm-pump. Therefore two monophyletic groups with alternative types of sperm-pumps (Fig. 25) are constituted: 'Petaluroidea' and 'Libelluloidea' (Fig. 26; for further synapomorphic characters of the sub-groups of the Libelluloidea – which, according to unpublished studies, also apply to the Cordulephyidae, Gomphomacromiidae and Synthemistidae – see Pfau 1971: 340).

Three distinct different types of glans have been found within the Anisoptera. Each seems to represent an attempt of a 'problem-solution', which must have arisen as the early anisopteran vesica spermalis had arrived at a certain level of differentiation. This level has been designated as 'pre-gomphaeschnoid'. The pre-gomphaeschnoid vesica spermalis of the Anisoptera must have been already equipped with an erectile organ to manage different (and partly contradictory) functions: to inflate the V4 (to anchor it inside the female vagina) and to cause dorso-ventral V4-movements. At that level, no direct functional connection existed between the compression of the erectile organ and the emptying process of the reservoir – these functions were only co-ordinated with respect to time. The functional independence of V4-inflation and sperm-transfer obviously only survived in the Gomphaeschnidae and Aeshnidae, which however used the co-ordinated movement of the V4-furrow to function as a 'two-way tap', implicating a close relationship between the function of the erectile organ and the pathway of sperm. The special importance of production of high-speed jets of sperm is apparent already in this system, since different characteristics, which point in this direction, have been added: closure of V3-furrow to a true tube (several genera); narrowing of the distal V3-furrow (or tube) to form a sperm-injector (*Aeshna cyanea*; *Caliaeschna microstigma*

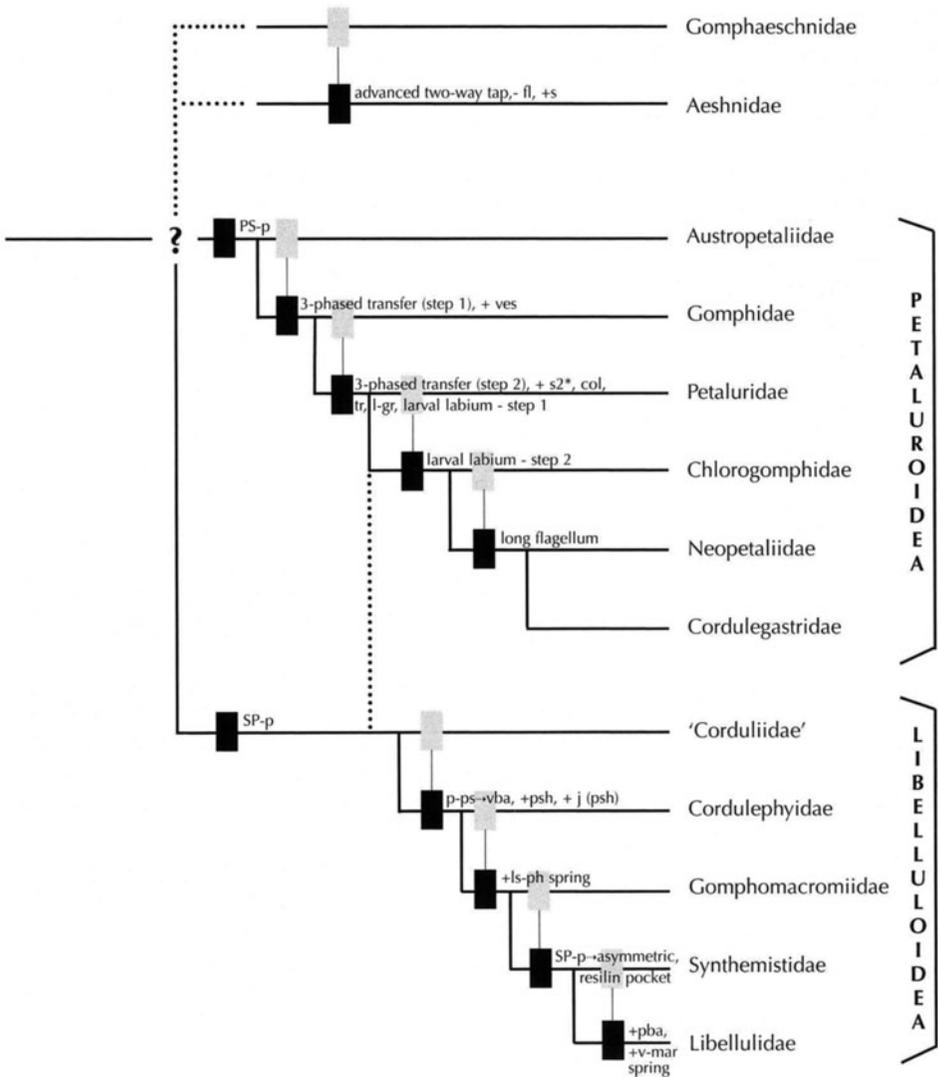


Figure 26: Phylogenetic arrangement of anisopteran subgroups, mainly according to the comparative functional morphology of the glans. — Apomorphic characters are shortly indicated: '+ ls-ph spring' e.g. indicates a newly evolved elasticity, which originates from flexible zones of the lateral sclerites and proximal horns of the processes 'f' (cf. text). The Chlorogomphidae have been placed on account of the 'spoon-shaped' larval labium, a character that is already detectable ('step 1') in the Petaluridae (G. Fleck pers. comm.). No possibility has been found to maintain a group 'Cavilabiata', which would afford a connexion of the Libelluloidea via the dotted line. The hitherto recognized Corduliidae (cf. Fraser 1957) are interpreted as a multiple paraphyletic group.

[Schneider] shows an extremely narrow jet nozzle at the distal end of its closed V3-tube, suggesting a functional correlation); narrow continuation of the V3-furrow (*Boyeria irene*, *Gomphaeschna furcillata*).

In the two other 'problem-solutions' (PS-pump and SP-pump) the function of the erectile organ has been directly connected to the process of reservoir-emptying: both types of sperm-pump support the emptying of the sperm-reservoir by sucking sperm from distally. And both are capable of producing an accelerated jet of sperm. Apparently in these cases a closed V3-tube was indispensable, and accordingly this character evolved multiple times. With respect to the efficiency of the sperm-pumps, the SP-pump of the Libelluloidea shows functional advantages compared to the PS-pump of the Petaluroidea: only in this type can elastic forces of the external cuticula be utilized to produce an especially high velocity of pump-cavity collapse. The SP-pump shows also clear advantages with respect to the capability for an extra large widening of the pump-cavity, since this is accomplished via the compression of the erectile organ. On the other hand, the circumstance, that the SP-pumps have a suction-effect during the compression-phase, can be evaluated as a fundamental advantage compared to PS-pumps, since sucking and closing of the dorsal V3/V4-cleft (s_2) are correlated – the sealing of the V4-furrow by an inflating tongue instead is presumably a late additional improvement. The difference in the efficiency of the two sperm-pump types is apparently reflected in the different duration of copulations: 70 minutes in *Cordulegaster bidentata*, but only few seconds in *Libellula quadrimaculata* (own unpubl. observations).

Besides the general acceleration in emptying the reservoir, the production of quick jets of sperm seems to have been favourable in all main groups to wash out foreign sperm. This is suggested by the jet-acceleration itself as well as by its retrograde guidance, accomplished by the V4-movement or special V4-structures, respectively. The fact that all main groups of Anisoptera seem capable of sperm displacement via washing-out raises the question, to what extent might the evolutionary success of the extant Anisoptera have depended on the acquisition of this ability. After attaining a certain level, three ways to manage a sperm-displacement via flushing could have been so superior compared to other systems that the latter evidently were outcompeted. Apparently no further system, pre-gomphaeschnoid or otherwise, reached the present. Nevertheless, to check this question, the large complex of 'aeshnoid groups' should be investigated thoroughly.

DISCUSSION

Observations and experimental difficulties

The simply organized sperm-reservoir of the V1 shows a thin cuticula and is easily compressible. In contrast, the erectile organ, including its external distal structures, is complex, with variably thick walls in different regions (cf. also Preliminary remarks). The hydraulic effect of the erectile organ on the structures of the glans depends on (1) the strength of the compression caused by the movement of the abdominal sternite 3; (2) the internal pressure of the erectile organ, which depends on the secretory activity of its wall-cells; and (3) the organization of the inflatable glans, e.g. the presence of a sperm-pump, the mobility of the V4 against V3 etc. Compared to the sperm-reservoir, the glans-structures are not uniformly thin: the

sperm-reservoir and the movable and inflatable parts of the glans exhibit different temporal constants. Since the erectile organ functions as an amplifier, which only acts on the glans and not on the sperm-reservoir, a possibility to tune different temporal constants to each other has been created by the evolution of the erectile organ. This could have been a functional necessity, and could furthermore have represented a functional prerequisite for the evolution of sperm-pumps.

Although direct measurements are lacking up to now, the inflation-experiments (squeezing of the V1) indicate, that the pressure inside the erectile organ of freshly killed anisopterans is rather low. It is obviously very low, if the time between capture and experiment is long. In this case an unnatural high pressure must be exerted on the V1 to achieve an inflation of the glans. Whereas the sperm of the easily compressible sperm-reservoir is immediately pressed distally, the reaction of the sperm-pump of the glans is delayed. In the Libellulidae it seemed to be too slow to activate a sufficiently strong suction effect. A large coherent string of sperm was expelled in *Orthetrum cancellatum* and *Libellula quadrimaculata* immediately after the beginning of the compression and during the whole period of inflation. According to the insufficient suction-effect of the SP-pump in experimental situations, large parts of sperm are obviously able to pass across the orifice of the sperm-pump chamber. Nevertheless, some sperm could be found afterwards inside the expanded SP-pump cavity.

The vesica spermalis of freshly killed specimens of *Cordulegaster boltonii* was manipulated and observed under water. Air, which was stored inside the PS-pump cavity, was pressed outside via the Pf₂ during each compression of the V1; a small amount was also expelled through slits lateral of the triangles, a small passage which is presumably not open normally, if the V4-apex is sufficiently lifted. Impregnations of the V4 with special fluids (e.g. glycerine) showed comparable results. When the pressure on the V1 was released, the immediately following suction effect indicates a widening of the walls of the sperm-pump on account of elastic properties: a backward directed effect on the air or glycerine could be observed. Even a small rotation of the V4 in its joints 'j v4' ventrally and then dorsally, led to a distinct decompression and compression of the PS-pump and to a suction and ejection, respectively, via the functional pore Pf₂. Similar effects were achieved, when the V4 itself was pressed and released at its rear or lateral sides. If the external cuticula was peeled off, the thin wall of the PS-pump could be manipulated directly, e.g. by using jets of a syringe. By this, the wall of the pump was dented inwards; it restored afterwards immediately its form, demonstrating elastic properties. These experiments clearly indicate a correlation between the PS-pump and the compression-decompression processes, which depends on the erectile organ-linkage between V1 and glans.

Furthermore, these experiments indicate, that hypotheses of Lohmann (1995), concerning the function of the PS-pump ('Ausspritzkammer', Pfau 1971, 1991; Lohmann's 'Buccula spermalis') as a storage chamber of foreign sperm, cannot hold true. Instead, the suction-effect of the PS-pump is expected to cause in each decompression-phase its own sperm, located nearby in the vestibule and/or V3-tube, to stream into the pump-cavity. It cannot be excluded that foreign or the individual's own sperm, accidentally positioned near the Pf₂ (i.e. outside the glans), may also be influenced, and is moved in the direction of the V4-furrow. In any case, sperm which had been sucked into the furrow from outside, will be expelled during the next compression.

As in the Aeshnidae (cf. *Boyeria irene*) the theoretical possibility exists in the Cordulegastridae, that movements of the V4 might also occur correlated in time to the 'wrong' phase: a V4-elevation e.g. might occur during decompression. This possibility would imply the necessity to assume, that (for instance) the ligula would be moved backward at that moment, causing a passive elevation of the V4 at the vaginal wall. Since the connection between the vestibule and the pump-cavity would be now closed, the suction-effect of the PS-pump would only affect sperm lying inside the V4-furrow and outside the V4, adjacent to the Pf₂; this sperm would be sucked 'backwards' into the PS-pump cavity. The following compression of a lowered V4 would expell that sperm, which had just been sucked in, only slowly, on account of a broad and undifferentiated 'functional pore': the sperm would flow as well inside as dorsal to the V4-furrow, and would also pass the transverse slit and enter the vestibule. This theoretical possibility is therefore excluded here. No indication has been found to substantiate Lohmann's intimation that the V4 would function as a depot-chamber for foreign sperm – filled during copulation and emptied afterwards outside the female vagina (see also below: Discrepant hypotheses). Although in several cases sperm could be found inside the PS-pump cavity of preserved specimens of the Petaluroidea (*C. boltonii*, *Petalura gigantea*, *Asiagomphus pryeri* (Selys), *Ictinogomphus ferox*), this can be interpreted, in contrast to Lohmann's hypothesis, as being due to the fact that the decompression-phase is the resting-phase of the PS-pump: some sperm may be automatically sucked into the pump-cavity, when the decompressing vesica spermalis is removed from the female vagina.

In the case of the SP-pump of the Libelluloidea there are different observations, which substantiate the succession of sperm-suction and discharge during a compression-decompression sequence. Experiments showed a distinct suction-effect of the SP-pump of *L. quadrimaculata* during compression, as soon as the string of sperm, caused by a first compression (cf. above), had passed the functional pore Pf₂: small amounts of fluid were then immediately sucked back into the V4 (during compression!). This fluid became then visible again at the Pf₂-orifice during the following decompression. This indicates that the SP-pump is in principle able to cause suction also on sperm that lies outside the vesica spermalis. However: since this way is long, and since the intact inflated tongue functions as a seal – i.e. a functional valve, closing the V4-furrow and improving the suction-effect of the SP-pump on sperm of the V3-tube and reservoir – this effect appears to be unnatural. External sperm, which should nevertheless be sucked proximally into the V4-furrow during compression, would in any case collide and combine with the sperm, which is at the same time pressed distally out of the V3-tube.

Seemingly the reasons, responsible for unnatural and non-consistent outcomes of sperm-flow experiments, are different: in the case of Libellulidae, an insufficient or late inflation of the tongue and a too slow widening of the sperm-pump cavity may be important. In other groups (e.g. Cordulegastridae) the prevention or wrong activation of the V4-movements during compression and decompression can apparently lead to an unnatural opening or closing of passages and valves, respectively. The fact that the experiments resulted in inconstant effects indicates unnatural experimental conditions, which also seem to originate from too strong squeezing-manipulations. In some experiments the squeezing of the V1 even drove the sperm outside the valve of the filling-pore of the reservoir (P₁) – this pore surely does not represent a functional pore of ejaculation.

Concerning an experimental proof, no method was found, to directly and constantly visualize the actual sperm-flow. A demonstration of the actual sperm-flow, and clarification of its role for the displacement of foreign sperm, seems to be opposed by several severe difficulties. One of these depends on our inexperience of the actual pressure-states inside the female vagina, which could be modified by muscular activities of the vaginal walls. Furthermore, the pressure inside the vesica spermalis (which is unknown) can possibly be modified by the male by further means, e.g. through movements of the ligula (cf. Pfau 1971: muscle 11). The actual pressure-events inside the glans seem also to be influenced by certain peculiarities of the V1-compression, e.g. by a bistable mechanism of the V1-piston (consisting of 'st 3' and 'm'; Fig. 1) in the Libelluloidea (Pfau 1971: 350), which should strongly influence the actual temporal completion of compression and decompression.

Discrepant hypotheses: function of the glans

Hypotheses of Lohmann (1995) concerning the functional morphology of the glans ('Bulbus vesicalis') and ensuing phylogenetic interpretations (Lohmann 1995, 1996) could not be confirmed. Lohmann e.g. (1) apparently followed discrepant interpretations concerning the erectile organ, ignoring the correlation of compression and decompression to V4-movements and (different) reactions of distal sperm-chambers – these chambers were treated all alike and redesignated as 'Buccula spermalis'; (2) took no notice of the vestibule present in most Petaluroidea; (3) overlooked the presence of passages between the V3-tube + V4-furrow and the SP-pump pouches (Lohmann's 'invaginierte Buccula spermalis') in the Synthemisidae; (4) differently interpreted the valve-function of the tongue ('Zungenventil') of the Austropetaliidae and Cordulegastridae. To substantiate his hypothesis of the 'Buccula spermalis' as a depot-chamber for foreign sperm, Lohmann needed additional ad hoc hypotheses, for which convincing arguments or supporting evidences are lacking.

The hypotheses of Lohmann (1995, 1996) and Miller (1990) – the latter author even denied the existence of sperm-pump chambers in Libellulidae – seem highly improbable based on present results. Their claims can be rejected by several aspects of functional anatomy, e.g. the non-existence of a functional pore between the processes 'f' in Cordulegastridae, the existence of a sperm-pump in the Libellulidae etc., and by observations during the inflation-experiments (cf. previous chapter).

Discrepant hypotheses: phylogenetic systematics

Different methods of scientific proceeding have led to several differing phylogenetic arrangements of anisopteran groups. In some cases the discounting, or at most only cursory consideration, of functional aspects is obvious, mainly concerning the complex apparatus of the odonates, i.e. the secondary copulatory apparatus, the flight apparatus and the cercal apparatus (Pfau 1971, 1986, 2000, 2002). It is not the purpose of this study to analyze the numerous conflicting interpretations that result from this. Only two examples will be examined, to illustrate the extent of disagreement and the necessity for further studies.

The much discrepant systematic arrangement of the anisopteran sub-groups of Carle (1995, 1996: 233f.) e.g. is confronted with some serious questions by the results on the vesica spermalis presented here. Following Carle's system, the gomphoid, petaluroid, cordulegastroid, neopetalioid and chlorogomphoid PS-pumps must be evaluated as primitive, since multiple convergence is unlikely. This 'primitive' PS-pump would then have been secondarily transformed into the 'two-way tap' of the Aeshnidae – reverting, in most genera, to the primitive (= open) condition of the V3-furrow – as well as into the SP-pump of the 'Libelluloidea'. Each transformation must have passed through a state without a sperm-pump. However, a reversal of the evolution is unlikely in this case of a functional significant organ and is especially unlikely in the case of an advanced type of PS-pump as starting point. Therefore an origin of the Libelluloidea from the base of Chlorogomphidae + Neopetaliidae + Cordulegastridae (dotted line in Fig. 26) is rejected. The comparative investigations instead indicate a persistent progressive evolution in the main groups.

Furthermore, the system of Carle implies at least three independent evolutionary derivations of the endophytic (orthopteroid) ovipositor: in the 'Zygoptera', Epiophlebiidae and the Aeshnidae + Austropetaliidae. One of the bases for Carle's view of evolution is, that "certain fossil 'Zygoptera' are characterized by exophytic ovipositors". There are however indications that the 'Zygoptera' represent a paraphyletic group (Fraser 1954, 1957; Pfau 2002), pointing out that the ancestor of the *Odonata was already an endophytic zygopteran (for structure and evolution of ovipositors, cf. Pfau 1985, 1991). With respect to the ovipositor, the phylogenetic system presented here affords the assumption of a convergent reduction of the female endophytic ovipositor in the Libelluloidea and the Petaluroidea (total loss presumably multiple). Concerning the spoon-shaped labial mask – a character, which has been used to constitute a group 'Cavilabiata' – a convergent evolution inside the Petaluroidea and at the base of the Libelluloidea is assumed.

The Neopetaliidae are classified, in contrast to Carle, where this group represents the sister group of the Chlorogomphidae + 'Libelluloidea', as the sister group of the Cordulegastridae, founded on the synapomorphic character 'long tongue'.

The phylogenetic system of Lohmann (1996) also reveals several disagreements; certain essential characters ('Bulbus vesicalis', 'entoflexate tibiae'), which have been used to substantiate anisopteran ramifications, obviously need a re-evaluation (see also previous chapter).

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