Evolution of the dragonfly head-arresting system

Stanislav N. Gorb†

Max-Planck-Institut für Entwicklungsbiologie, Spemannstrasse 35, Tübingen D-72076, Germany (stas.gorb@tuebingen.mpg.de)

The arrester or fixation system of the head in adult Odonata is unique among arthropods. This system involves the organs of two body segments: the head and the neck. It consists of a skeleton–muscle apparatus that sets the arrester parts in motion. The parts comprise formations covered with complicated microstructures—fields of microtrichia on the rear surface of the head and post-cervical sclerites of the neck. The arrester immobilizes the head during feeding or when the dragonfly is in tandem flight. Thus, it may serve as an adaptation to save the head from violent mechanical disturbance and to stabilize gaze in a variety of behavioural situations. This study shows the evolutionary trend of the arrester in the order Odonata by using scanning electron microscopy and measurements of arrester structures in 227 species from 26 odonate families. The arrester design occurring in the Epiophlebiidae, Gomphidae, Neopetaliidae, Petaluridae and Chlorogomphinae is suggested to be the basic one. Two convergent pathways of head-arrester evolution among Zygoptera and Anisoptera are proposed. The possible functional significance of the arrester system is discussed.

Keywords: cuticle; microtrichia; head–neck articulation; attachment; Odonata; evolution

1. INTRODUCTION

The design of the head–prothorax transition in adult Odonata does not have any analogues in other groups of insects. The area involved in the articulation of the head with the neck is very small compared with the head dimension; it is virtually a single point providing high head mobility in the roll, pitch and yaw planes (Mittelstaedt 1950). Such mobility of the head compensates for the absence of a specialized gravity organ. The head is analogous to a statolith, the movements of which are monitored by the head, neck and prothoracic fields of the hair sensilla. At the same time, such a design of the head–neck articulation has weak mechanical strength. The head, however, should be rigid with the rest of the body as, for example, during feeding, to prevent disturbance caused by the big mandibular muscles and to stabilize gaze while perching or holding prey in flight. During the initial stage of tandem formation, the male holds the female by the head in order to grasp the head or prothorax with its appendages (Gorb 1996a). This usually happens in flight and at high speed and one may expect high loads on the head during such manipulations. In addition, males hold females by the head (Anisoptera) or prothorax (Zygoptera) in tandem flight during copulation when the two animals are paired. In such a position, the female head can be easily damaged when it is not rigidly connected to the thorax (Wildermuth 1984). The arrester thus serves to immobilize the head during feeding or when the dragonfly is in tandem flight. The arrester

system includes the adjusting organs of two body segments—the head and neck—and consists of (i) the skeleton–muscle apparatus that moves the head and neck sclerites, (ii) co-opted microsculptures, which are fields of microtrichia on the rear surface of the head (MFH) and on the post-cervical sclerites of the neck (SPCs), (iii) the secretory apparatus consisting of epidermal cells, which produces lipid substances which pass through porous channels in the cuticle into the region of contact between the MFH and SPCs, and (iv) sensory organs monitoring contact between the MFH and SPCs and the position of the SPCs relative to the other neck sclerites (Gorb 1991a).

The first report on the arrester system was by Berlese (1909), who described and illustrated the neck sclerites and MFH as a functional system. He presumed that it was a stridulation organ. Tillyard (1917) doubted this function and later Mittelstaedt (1950) suggested a fixation function for these organs and called this system an ‘arrester’. The arrester remained a little-known structure until recently. However, study of the arrester may be of general interest, because of the microtrichia-covered surfaces providing fixation due to high friction between interlocked microstructures in the contact area. Such design seldom occurs among biological attachment systems. Moreover, the arrester characters, which are specific at family and subfamily levels, may be useful for suprageneric systematics and phylogenetic reconstruction. This work was undertaken to investigate the evolutionary pathways of the arrester system among Odonata. In addition, it briefly summarizes previous studies on skeleton–muscle organization (Gorb 1989, 1993), inner morphology and ultrastructure (Gorb 1990b, 1997a,b), the microsculpture of the frictional surfaces (Gorb 1990a,c), the physiology of flight reflexes connected to the arrester

†Present address: Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität, Erbertstr. 1, Jena 07743, Germany (b6gost@pan.zoo.uni-jena.de).

(Gorb 1991b) and the sensory organs involved in arrester monitoring (Gorb 1991a).

2. MATERIALS AND METHODS

Representatives of 227 species from 26 odonate families of the world fauna were studied (Calopterygidae, Chlorocyphidae, Dictyristidae, Diphlebiidae, Euphaeidae, Polythoridae, Rimanelidae, Chlorolestidae, Lestidae, Megapodagrionidae, Perilestidae, Hemiphlebiidae, Coenagrionidae, Isostictidae, Platynemididae, Platystictidae, Protoneuridae, Pseudostigmatidae, Epiophlebiidae, Aeshnidae, Gomphidae, Neopetaliidae, Petaluridae, Cordulegastriidae, Corduliidae and Libellulidae). Unfortunately, the idea of studying the arrester system in fossil Odonata failed, because the necks of most specimens studied have been usually covered by the head capsule. In addition, even in the best casts the microstructure of the stone did not make it possible to recognize microtrichia on the head and neck.

(a) Preliminary preparations and study under the binocular microscope

The rear surface of the head and the SPCs were drawn using the eyepiece grid of the binocular microscope. These pictures were later used for measurements of the arrester characters. The head and SPCs were treated with a 10% aqueous solution of KOH at 100 °C for 0.5 h, washed, dehydrated in ethanol and xylol and embedded in Canada balsam.

(b) Morphometry

In order to study the interdependence of some characters of the macrosculpture of the head capsule, four distances were measured: head width, arrester basis (distance between the left and right MFHs), length of the MFH and width of the MFH. Since the variability of these characters was rather low within species (Steinmann 1967), it was only possible to use one to two specimens of each species studied.

(c) Scanning electron microscopy

For scanning electron microscopy (SEM) the desired pieces of dry material were prepared, mounted on holders, sputter-coated with gold or gold-palladium (100–150 Å) and examined using scanning electron microscopes: JEOL JSM-35 (Institute of Botany, Kiev), JEOL JSM-T20 (Institute of Material Sciences, Kiev), TESLA BS-301 (Institute of Zoology, Kiev) and HITACHI S800 (MPI für Entwicklungsbiologie, Tübingen).

3. SKELETON-MUSCLE ORGANIZATION OF ARRESTER SYSTEM

The lateral walls of the imaginal neck consist of a pair of eucervical sclerites (SECs) (figure 1), which are symmetrical relative to the longitudinal body axis. Anteriorly, they transform into two sharp processes called cephaligers (CEPs). These processes meet at their extreme anterior point, which is the centre of mass of the head. At this point, the tentorium, the skeleton of the head, is connected to the neck through a pair of mobile joints. Ventrally, the SECs are connected to the basisternum (BS) through the neck membrane, which is elastic and has particular folding properties. These properties are reflected in the complex fine structure of the neck membrane, providing high mobility of the SECs. Near their dorsoproximal edges, the SECs are connected to the

Figure 1. Neck region of the libellulid dragonflies. (a) *Sympetrum sanguineum* (Anisoptera, Libellulidae), dorsal view. (b) *Orthetrum cancellatum* (Anisoptera, Libellulidae), lateral view. a, anterior direction; BS, basisternum; CEP, cephaliger; CX1 and CX2, coxae; d, dorsal direction; JT, joint between prothorax and eucervical sclerite; l, lateral direction; NM, neck membrane; OCC, direction to the occiput; PN, pronotum; PT, prothorax; SEC, eucervical sclerite; SPC, post-cervical sclerite.

SPCs. The latter are isolated from the SECs and surrounded by the neck membranes on three sides. Such an articulation enables very high mobility of the SPCs. Each SPC is differentiated into a sclerotized base and an elastic distal region, which is covered by microtrichia and provided with both hair and campaniform sensilla (Gorb 1991a).

The muscle system of the neck–head transition is rather similar in many insect groups and consists of three pairs of muscles responsible for head movements in three

Figure 2. *Sympetrum sanguineum* (Anisoptera, Libellulidae) skeleton-muscle organization of the arrester system, medial aspect. *a*, anterior direction; *d*, dorsal direction; BS, basisternum; CEP, cephaliger; MI, abductor of the SPC; PN, pronotum; SEC, eucervical sclerite; SPC, post-cervical sclerite.

planes (roll, pitch and yaw) (Pringle 1963; Strausfeld *et al.* 1987). In Odonata, there is a pair of abductor muscles (MI) involved in the control of the SPCs (figure 2). The origin of an abductor muscle is an apodeme of the pronotum (PN). The insertion is located in the proximal region of the SPC between both the SEC and SPC (figure 2). The location of the insertion is rather similar in all odonate taxa studied. However, the apodeme of the PN is pronounced differently in representatives of different taxa. In the series of species *Cordulegaster*, *Sympetrum*, *Cordulia*, *Aeshna* and *Gomphus*, the apodeme tends to elongate. This can result in a different direction of the muscular force depending on the relative positions of the origin and insertion. When the abductor muscles contract, the SPCs move medial to the longitudinal body axis and lose contact with the microtrichia fields (the head is free). This movement provides the undoing of the arrester system when the animal needs to move its head. The antagonistic muscle responsible for SPC adduction was not found; thus, the SPC adduction is passive. In the SPC-SEC transitional area, there are a few regions of cuticle with high elasticity due to peculiarly organized cuticular structures. These are cuticular 'springs', which can return the SPC to the lateral position when the abductor muscle relaxes. The elastic cuticle of the distal part of the SPC is adapted to provide soft contact with the MFH.

The MFHs on the rear surface of the head and the SPCs covered with microtrichia are functionally corresponding structures, corresponding in the shape, size and density of microtrichia (figure 3*a-e*). However, the MFHs differ in their size and location in representatives from different families. It can be hypothesized that these parameters may depend on the construction of the head capsule. To test this hypothesis, morphometric characters of the head in 227 representatives from 26 odonate families were studied. In insects, the relation of the head width to the occiput width is usually two- to fourfold. In adult Odonata, this relation varies from eightfold in the Petaluridae to 16-fold in the Hemiphysidae. When the

head is fixed to the neck on MFH points, the head obtains two additional points of contact with the neck area. This provides higher stability of the head. An analysis of our measurements shows that the distance between the left and right MFHs (the arrester basis) correlates with head width; the relationship is linear (figure 4). However, for seven Odonata families, the evaluated slopes of these lines were different (table 1). This fact can be explained by constructional differences of the head capsule. Surprisingly, the MFH size is weakly dependent on head width (figure 4 and table 1). The correlation for Corduliidae is very low compared with that for all the other families. A possible explanation is that the measured sample of representatives of this family was very small.

4. FUNCTIONAL SIGNIFICANCE OF THE ARRESTER

Electrophysiological recordings of flight muscle activity with simultaneous photodiode registrations of SPC movements showed that the release of the head was synchronized with the initiation of wing muscle activity only when flight was elicited by substrate removal or a wind pulse (Gorb 1991*b*, 1995) (figure 5). However, the head-arrester system can work independently of the wing apparatus in at least two behavioural situations (Gorb 1991*b*). These are while eating or flying in tandem, when a dragonfly shows wing muscle activity even while the head is arrested.

Dragonfly legs serve as a basket trap which is used for prey capture or mate holding during flight. When a dragonfly captures prey, its front legs bring the victim to the mouth. Dragonflies tear apart the prey by mandibles and pull it down by the forelegs. This must require a highly efficient locking mechanism by the neck so that the dragonfly does not pull off its own head when eating. Complex flight manoeuvres have not been observed in flying dragonflies holding prey. A dragonfly uses gliding flight when feeding on the wing. The reason why an insect does this is that the high-speed manoeuvres are possible only when the head is free and serving as a gravity organ controlling turn performances during flight. Other foreleg action that would perturb head position in flight is when the insect cleans its eyes. Presumably, the head is also arrested in this situation.

In tandem, the female head is arrested to prevent cases of head damage during the initial stages of copulation or in tandem flight. Such cases have been described for gomphids (Dunkle 1984) and libellulids (Wildermuth 1984). Thus, the arrester system may serve as an adaptation to save the head from violent mechanical disturbances and to stabilize gaze in a variety of behavioural situations.

In addition, the arrester system has a sensory function. Loss of SPC-head contacts elicits activity of the wing muscles: in experiments in which the head was pulled away anteriorly with a micromanipulator and SPC-head contact was lost, the resting dragonfly initiated flight. This behaviour is under the control of both campaniform and hair sensilla of corresponding structures of the head. It has been previously hypothesized that the arrester sensilla are an additional link within the sensory loop controlling flight in the Odonata (Gorb 1991*a,b*).

Figure 3. *Zygonyx ida* Selys (Anisoptera, Libellulidae). (a, c and d) Left SPC, and (b, e) left field of microtrichia on the rear surface of the head. a, anterior direction; d, dorsal direction; l, lateral direction; SEC, eucervical sclerite; SPC, post-cervical sclerite. (c, d) Magnified areas marked in (a) as boxes C and D, respectively. (e) Enlarged region of the microtrichia field in (b).

An intriguing idea explaining the arrester-system function in Anisoptera has recently been proposed (Beckemeyer 1997). Since the male has firm hold of the female head capsule, he can more easily control her flight. He controls the orientation of the flight directional sensor—the head—and, in essence, forces the female to fly in formation, not only by mechanical contact, but by direct manipulation of the flight control and steering system of the female. However, the female's head is arrested in tandem, as indicated above. Although Beckemeyer (1997) did not take into account the arresting of the female head, it is plausible that flight control may also be possible when the female's head is fixed by the SPCs because the arrester sensilla may be involved in control of female flight in tandem.

5. HEAD MOBILITY AND HEAD STABILITY: A COMPARISON WITH OTHER INSECTS

Dragonflies have several characteristics, such as the male secondary copulation organs and larval mask, that are unique among insects (Tillyard 1917). The relative dimensions and weight of the head in adult dragonflies surpass those of many other insects. It may be suggested that the ability to perform head movements in every plane in space is provided by a highly developed neck area. Indeed, adult Odonata have large cervical (neck) sclerites when compared with those of other insects or even with odonate larvae (Snodgrass 1909; Crampton 1926; Asahina 1954; Popham & Bevans 1979). The larval head has a larger basis of articulation to the prothorax

Figure 4. Dependence of some arrester characters on the head width. (a) Measurements used: b , arrester base or the distance between microtrichia fields (MFH); s_1 , height of the MFH; s_2 , width of the MFH. (b) Dependence of MFH size (s_1 and s_2) and arrester base on the head width. Data on representatives from seven odonate families (Gomphidae, Aeshnidae, Corduliidae, Libellulidae, Calopterygidae, Lestidae and Coenagrionidae) have been used.

when compared with the imaginal one. The head mobility in the larva is lower, because the larval head is firmly connected to the thorax to maintain stability during powerful predatory strikes (Olesen 1972; Tanaka & Hisada 1980; Parry 1983). The larval neck is small, the cervical sclerites are tiny and the SPCs are fused with the SECs (Crampton 1926). In the adult, the prey is mainly captured by the front legs and the mouth parts no longer seem to be involved in prey capture. The neck sclerites, which are specialized for head fixation, are found only in adult Odonata. The SPCs of representatives of the closest groups to odonates, Ephemeroptera and Plecoptera, are very small and not specialized for head fixation. Clearly cut fields of micro-outgrowths on the rear surface of the head are absent in odonate larvae and in representatives of Ephemeroptera and Plecoptera as well.

Many other insects have big heavy heads and most insects that fly need to have independent head movements (Olberg 1978, 1981; Olberg & Pinter 1990). For example, mantids have exceptionally high mobility of the head (Liske 1982, 1984, 1989; Liske & Mohren 1984; Liske & Davis 1986), but do not possess a specialized head-arresting system like that of Odonata. Being ambushing predators, mantids do not feed on the wing like dragonflies and do not escape immediately when disturbed by predators. Therefore, mantids may not need such a specialized gaze stabilization device as dragonflies. Nor do mantids employ tandem formation during copulation. Dragonfly males hold females by the head; even damselfly males hold the female's head during the initial stage of tandem formation (Gorb 1996a).

It seems that the arrester system is an autapomorphy of the Odonata. It is suggested that arrester evolution was connected to the evolution of the odonate copulative process, which is one of the most unusual among Insecta due to specialized male copulative organs and tandem postures during copulation. An additional selective pressure that has contributed to the evolution of the arrester system, which prevents head disturbance and stabilizes gaze, might have been the evolution of Odonata as active flying predators that often feed on the wing.

In some representatives of Insecta, head-arresting systems, which are completely different from those of odonates, are known. While cutting a plant stem, representatives of Isoptera lock the head to the thorax using mandibular locking devices (Ilychev 1987). In dipterans, the head is also very mobile (Sandeman & Markl 1980). The range of head turns in the blowfly *Calliphora* is $\pm 20^\circ$ both horizontally (yaw) and vertically (pitch), and $\pm 90^\circ$ for rotations about the line of sight (roll) which roughly corresponds with the main body axis (Hengstenberg 1991). Head stability in some taxa of flies is presumably provided by armoured membranes (Gorb 1997c).

The odonate arrester is a unique fixation system owing to the following features. First, the head-arresting systems, designed as mobile neck frictional devices, have not been previously reported in representatives of other orders of insects. The second feature is an absence of antagonistic muscles, which are normally involved in mobile structures of most arthropods. Such an absence is usually compensated by different hydraulic adaptations, such as the odonate larva mask (Olesen 1972; Tanaka & Hisada 1980), spider legs (Foelix 1982) or by elastic springs, such as in the cranio-mandibular system of the Dacetini and Odontomachini ants (Dlussky & Fedoseeva 1988), insect pretarsus (Gorb 1996b) and fly labellae (S. N. Gorb, unpublished data). In the arrester system, the SPC-SEC transitional area is elastic and acts as an antagonist to the SPC abductor muscle.

The third unique feature is a variety of modifications of fixation type within the Odonata. The fixation type depends on the structure of the microtrichia on the corresponding surfaces of the head and neck (figure 6). Four sets of correlating microtrichia types occur: (i) hook-like or cone-shaped microtrichia and mushroom-like microtrichia (*Sympecma*, Libellulidae), (ii) cone-shaped microtrichia and thin seta-like microtrichia (Aeshnidae), (iii) mace-like microtrichia on both surfaces presumably acting like an elastic snap (*Lestinae*), and (iv) smooth surface and compressed microtrichia (Gomphidae, Petaluridae). This may explain the low dependence of the MFH size on the form and size of the head (figure 4). Presumably, attachment stability is provided by different fixation types and not by an increase in the area of contact. The contact performance is additionally supplemented by adhesive secretions delivered through a porous channel system in the contact area (Gorb 1990b, 1997b).

6. ARRESTER AND EVOLUTION OF ODONATA

In odonate classification systems (Tillyard 1917, 1928; Martynov 1924; Fraser 1957; Kiauta 1968; Pfau 1971, 1986, 1991; Pritykina 1980), sets of characters of different organs

Table 1. *The results of regression analysis of the arrester characters*

(Pearson correlation coefficient, slope of the line of linear regression and the coordinate of intersection of the regression line with the *y*-axis calculated for representatives of seven odonate families. *n*, number of species measured. *F*, d.f. and *p* are results of ANOVA between measured values and values calculated using linear regression analysis. The correlations in the lower part of the table are across all families.)

	Pearson correlation coefficient	slope (°)	<i>y</i>	<i>n</i>	<i>F</i>	d.f.	<i>p</i>
arrester base (<i>b</i>) versus head width							
Coenagrionidae	0.961	18.41	−0.418	8	73.07	6	0.000
Lestidae	0.775	15.17	−0.075	8	9.01	6	0.024
Calopterygidae	0.793	9.47	0.978	13	18.61	11	0.001
Gomphidae	0.907	29.10	−1.736	16	64.66	14	0.000
Aeshnidae	0.856	16.50	0.469	10	22.02	8	0.002
Corduliidae	0.214	8.10	2.647	4	0.10	2	0.786
Libellulidae	0.834	13.80	0.253	20	40.97	18	0.000
<i>b</i> , <i>s</i> ₁ and <i>s</i> ₂ versus head width							
arrester base (<i>b</i>)	0.967	22.36	−0.870	27	357.90	25	0.000
height of the MFH (<i>s</i> ₁)	0.771	6.60	−0.049	27	36.74	25	0.000
width of the MFH (<i>s</i> ₂)	0.844	4.75	−0.169	27	61.88	25	0.000

Figure 5. Scheme of diverse behavioural situations when the head is free or fixed by the arrester system. (1) Tandem sitting, (2) perching and roosting, (3) saccadic head movements during ambushing, (4) feeding, (5) flying with captured prey, (6) patrolling flight, and (7) tandem flight. Shaded quadrants indicate that the head is fixed by SPCs. Clear quadrants indicate that the head is free. Arrows indicate fixation (black arrowheads) or release (white arrowheads) of the head during the transition from one behavioural situation to another.

are used. Nevertheless, the phylogeny of the Odonata is mainly based upon wing characters or on those of the genitalia. A preliminary comparison of the head characters in representatives of a few odonate families was made by Steinmann (1967). The present study aids in understanding the evolution of the arrester system and provides information for further phylogenetic reconstructions as

well. Some arrester characters, such as the shape of the SPC and the MFH morphology, demonstrate a rather low variability at both family and subfamily levels. For the scheme of arrester evolution the following characters were used: the presence, number and location of the microtrichia fields of the head, the shape of the SPCs, their separation from the SECs and the shape, size, density and

Figure 6. Schemes of corresponding frictional surfaces occurring in odonate head-arrester systems. (a) Spines, plates system of libellulids. (b) Spines, filaments of aeshnids. (c) Clavate MT of lestids. (d) Leaves, smooth surface of gomphids.

location of microtrichia on the SPCs and in the microtrichia fields of the head.

(a) *Zygoptera*

The head is mediolaterally widened. There are three basic types of MFH design. The Coenagrionidae type (figure 7a) is characteristic of all Coenagrionoidea and some members of other families of the suprafamily Calopterygoidea (Polythoridae, Chlorocyphidae). Lateral to the occiput there are two isolated MFHs, ventral and dorsal, on each side. The Lestidae type (figure 7b) is characteristic for suprafamilies Lestoidea and Hemiphlebioidea and for some families of the Calopterygoidea (Euphaeidae, Diphlebiidae and Dicteriastidae). There is one clear isolated MFH on each side of the occiput. The Calopterygidae type (figure 7c) was found only in Calopterygidae. On the rear surface of the head there are no clear isolated MFH, all this surface being covered by micropapillae or short microtrichia (Gorb 1990a,c). In addition, calopterygids have small, weakly separated SPCs. Fixation probably takes place in the region of small depressions lateral to the occiput. It can be hypothesized that these characters are basic in the design of the arrester system of Zygoptera and that the Calopterygidae type is the most ancestral one among the Zygoptera. Since arrester and other structures of the head have been developed in parallel during evolution, Steinmann's (1967) data on the head morphometry may support the idea that the calopterygid head capsule is very basic among the Odonata.

In calopterygids, the rear surface of the head is completely covered by scattered micropapilla. These might serve for short-term head fixation at any point on the rear surface of the head. High-speed film taken in the field by G. Rüppell and D. Hilfert (unpublished data) has clearly demonstrated how *Calopteryx* males crash into each other during flight to remove other males from their tandem position with a female. G. Rüppell (unpublished data) hypothesized that aggressive behaviour of males

may be an additional situation during which the arrester system is used for the short-term fixation of the attacking male's head to prevent its mechanical damage. This explains well the design of microtrichia coverage of the head in Calopterygidae. Large areas of micropapilla on the back surface of the head seem to be better adapted to perform an extremely quick fixation release of the head.

Among the Zygoptera, two main directions in the evolution of arrester design can be distinguished from the basic Calopterygidae type (figures 7 and 9). The first (the Lestidae type) has resulted in one clearly defined field on each side of the head (Lestidae, Chlorolestidae, Hemiphlebiidae, Megapodagrionidae, Euphaeidae, Diphlebiidae and Dicteriastidae). The Diphlebiidae have a clearly cut field of micropapillae on the head. This character of the arrester system is transient between Calopterygidae and Lestidae. The representatives of the Lestoidea and Hemiphlebioidea are very similar to each other. All studied species from these suprafamilies have the Lestidae type of arrester design. Our data support the conclusion about the close relationship between the Lestidae and Chlorolestidae (Tillyard 1917) and about the close relationship between the Lestidae and Megapodagrionidae (Fraser 1957).

The second direction (Coenagrionidae type) has resulted in two clearly defined fields on each side of the head (Protoneuridae, Platynemididae, Coenagrionidae and Pseudostigmatidae) (figure 9). The dorsal field is smaller and usually contains shorter microtrichia than does the ventral field. In addition, the rear surface of the head contains the cuticular comb located medial to the fields of microtrichia. The comb is often covered by microtrichia and presumably serves as a stop for the SPCs. The representatives of Coenagrionoidea are rather similar in the design of the arrester. The Protoneuridae, Platynemididae, Coenagrionidae and Pseudostigmatidae have differences in microtrichia morphology; however, the general design of the arrester system remains

Figure 7. Morphological types of microtrichia fields on the head in Calopterygoidea (Zygoptera). (a) *Rhinocypha fenestrella* (Chlorocyphidae). (b) *Epallage fatime* (Euphaeidae). (c) *Calopteryx splendens* (Calopterygidae). oc, occiput; mp, mouthparts. Light grey areas indicate sparsely scattered micropapillae (p). Dark grey areas indicate microtrichia fields (mfh).

similar. There are some scale effects on the arrester macrostructure and also on the microtrichia. In large pseudostigmatids, the absolute area of the fields of the head is larger than in very small representatives of the Protoneuridae. However, the density of the microtrichia is usually lower and the size is larger in large species.

Some transitional characters from the Calopterygidae type to the Coenagrionidae type occur in representatives of the Hetaerinae (Calopterygidae). In *Hetaerina* spp., areas of longer micropapillae occur in the medial part of the rear surface of the head. A further stage in the field development and micropapillae elongation occurs in Polythoridae, Chlorocyphidae and Rimanellidae. In the series

Figure 8. Morphological types of microtrichia fields on the head in Anisoptera. (a) *Cyclophylla modesta* (Gomphidae). (b) *Rhyothemis variegata* (Libellulidae). (c) *Anax imperator* (Aeshnidae). oc, occiput. Dark grey areas indicate microtrichia fields (mfh).

Figure 9. Scheme of the possible paths of evolutionary changes of the arrester system. It is hypothesized that the basic type of arrester system is one with a smooth rear surface of the head. Sparsely distributed micropapillae covering large areas on the head were transformed into compact fields densely covered with microtrichia. In some families of Anisoptera and Zygoptera, each field convergently divided into two: a dorsal field and a ventral field.

of taxa Calopterygidae, Hetaeriniinae, Chlorocyphidae and Coenagrionidae, continuous transition of the head characteristics occurs. In most of the Coenagrionoidea, the characteristics of the Calopterygidae type, such as micropapillar coverage of the head, are lost. A very reduced remainder of the coverage was found in species of the genus *Copera* (Platynemididae and Calicnemidinae). Our data support the conclusion about the close relationship between the Pseudostigmatidae and Coenagrionidae plus Protoneuridae plus Platynemididae (Tillyard 1917). Thus, the main trend in arrester evolution is the loss of the micropapillar coverage of the rear surface of the head and the development of clearly defined fields of long microtrichia with very diverse shapes.

The Calopterygoidea is the least uniform suprafamily. The representatives of the different families in it show significant differences from each other. Some calopterygoid families are very similar to families from the Lestoidea or Coenagrionoidea. Hence, we cannot agree with the creation of the suborder Caloptera Zalessky (Zalessky 1932; Belyshev 1973). The similarity of head characters in the Euphaeidae to those in the Lestoidea may support the point of view that these taxa are much more closely related, as is stated in the most common phylogenetical reconstructions. Data on the morphometry of the head characters (Steinmann 1967) and on behaviour (Heymer 1975) support this conclusion.

(b) *Anisozygoptera and Anisoptera*

The head is nearly oval and widened mediolaterally. There are three basic types of MFH construction in Anisoptera (figures 8 and 9). The Gomphidae type is characteristic of the Epiophlebiidae, Gomphidae and Petaluridae (figure 8a). The shape of the head varies from widened mediolaterally (*Epiophlebia*, *Gomphus* and *Sinogomphus*) to lengthened dorsoventrally (*Phenes* and *Uropetala*). Lateral to the occiput there is a cuticular surface sparsely covered by microtrichia and hair sensilla. Clear-cut MFHs are absent. The Libelluloidea type is characteristic of Cordulegastridae, Aeshnidae and Libelluloidea. There is one clearly isolated MFH on each side of the head lateral to the occiput at the level of its ventral edge (figure 8b). The Anactini type is characteristic only of representatives of Anactini. The head capsule is similar to that in the Aeshnidae. However, there are two MFH on each side of the head (figure 8c).

Since specialized MFH are absent in most insects, it can be suggested that arrester evolution has been directed from a smooth surface or one sparsely covered with micropapillae to the formation of the microtrichia fields. If this is correct, then the Gomphidae type should be defined as the basic type of the arrester system. This occurs in Epiophlebiidae, Gomphidae, Neopetaliidae, Petaluridae and Chlorogomphinae. Species in this group have fields covered with trichoid sensilla and sparsely

distributed microtrichia. Presumably, the SPCs in their lateral position can touch these fields, when the head is in the most posterior position. It is also suggested that the compressed, leaf-like microtrichia of the SPCs, which were found in these taxa, may adhere to the smooth surface of the head. An additional adaptation for the fixation of SPCs on the smooth surface of the head is the particular shape of SPCs, which are lengthened along the dorsoventral axis.

The Chlorogomphidae is a transitional group between the Gomphidae and the Cordulegastridae. Its fields of cone-shaped microtrichia on the rear surface of the head have a denser pattern than in representatives of the Gomphidae. The head of Cordulegastridae still has the cuticular folds, which are very common among representatives of the Gomphidae and well-developed MFHs, which are characteristic of the Aeshnidae and Libelluloidea. The Libelluloidea (Corduliidae and Libellulidae) is a very uniform group according to its arrester characters. The cone-shaped microtrichia, which have been found on the head fields in most studied representatives of this suprafamily, resemble those of the Cordulegastridae. The same origin of this character can be hypothesized in the Corduliidae and Libellulidae. The main common characteristic of the Corduliidae and Libellulidae is the comma-like shape of the MFHs.

The proposed evolutionary path of the arrester system within the suborders Anisoptera and Anisozygoptera is in many ways similar to the scheme of Odonata phylogeny proposed by Fraser (1957) and to the scheme of the evolution of the chromosome complexes outlined by Kiauta (1968).

The preceding discussion focuses mainly on the structural evolution of a functional system. However, it cannot yet be determined how taxonomic differences regarding arrester structure relate to taxonomic differences regarding dragonfly behaviour. In future, one way to analyse the functional significance of different arrester systems will be the use of high-speed cinematography for comparative studies of flight behaviour amongst different odonates. However, even without this information, the present results demonstrate that morphological analysis of the arrester system can usefully contribute to phylogenetic reconstructions of the most natural scheme of relationships within the Odonata.

The author is most grateful to Professor Dr L. I. Frantsevich (Institute of Zoology, Kiev) and Professor Dr G. I. Shcherbak (Department of Zoology, University of Kiev), who supported this work. Dr L. N. Pritykina (Paleontological Institute, Moscow) provided consultations on odonate phylogeny. Discussions with Professor Dr U. Schwarz (Max-Planck-Institute of Developmental Biology, Tübingen), Professor Dr G. Rüppel and Dr A. Martens (University of Braunschweig), Dr G. Bechly (Specialist Group of Systematic and Phylogenetic Odonatology) and Dr M. Lindeboom (International Dragonfly Fund) are greatly acknowledged. The linguistic and stylistic suggestions made by Dr H. Silyn-Roberts (University of Auckland) helped to improve the English version of the manuscript. The author also wishes to thank three anonymous reviewers for criticism. This work was supported in part by a Max-Planck-Fellowship of the Schloßmann Foundation.

The following specialists and institutions kindly provided specimens for this study: Dr L. N. Pritykina (Paleontological

Institute, Moscow, Russia), Professor Dr A. Yu. Haritonov (Biological Institute of the Siberian Branch of Russian Academy of Sciences, Novosibirsk, Russia), Dr S. N. Borisov (Institute of Zoology and Parasitology, Dushanbe, Tadjikistan), Dr R. S. Pavljuk (Zoological Museum of the University Lviv, Ukraine), Dr L. A. Zhiltsova (Zoological Institute of Russian Academy of Sciences, Sankt-Peterburg, Russia), Professor Dr N. N. Shcherbak (Zoological Museum, Kiev, Ukraine), Dr J. DeMarmels (University of Central Venezuela), Professor Dr M. Samways (University of Natal, South Africa), Mr M. Sugimura (Tombo Ohkoku, Nakamura City, Japan), Dr C. Cook (Kansas City, USA) and Dr S. W. Dunkle (Florida State Collection of Arthropods, USA).

REFERENCES

- Asahina, S. 1954 *A morphological study of a relic dragonfly* *Epiophlebia superstes Selys* (Odonata; Anisozygoptera). Tokyo: The Japan Society for the Promotion of Science.
- Beckemeyer, R. 1997 Functional morphology of tandem flight in Odonata. *Argia* **9**, 13–17.
- Belyshev, B. F. 1973 *Dragonflies of Siberia*, vol. 1, parts 1 and 2. Novosibirsk: Nauka. (In Russian.)
- Berlese, A. 1909 *Gli Insetti*, vol. 1. Milano.
- Crampton, G. C. 1926 A comparison of the neck and prothoracic sclerites throughout the orders of insects from the standpoint. *Trans. Am. Entomol. Soc.* **52**, 192–248.
- Dlussky, G. M. & Fedoseeva, E. B. 1988 Origin and early stages of evolution of ants (Hymenoptera, Formicidae). In *Cretaceous biocoenotical crisis and insect evolution*, pp. 16–62. Moscow: Nauka. (In Russian.)
- Dunkle, S. W. 1984 Head damage due to mating in *Ophiogomphus* dragonflies (Anisoptera: Gomphidae). *Not. Odonatol.* **2**, 63–64.
- Foelix, R. F. 1982 *The biology of spiders*. Cambridge, MA and London: Harvard University Press.
- Fraser, F. C. 1957 A reclassification of the order Odonata. *R. Zool. Soc. NSW*, 1–133.
- Gorb, S. N. 1989 Functional morphology of the arrester-system in Odonata. *Vestnik Zool.* **N3**, 62–67. (In Russian.)
- Gorb, S. N. 1990a Microsculpture of the head fixation system of dragonflies in scanning electron microscopy. *Zool. Zh.* **69**, 148–154. (In Russian.)
- Gorb, S. N. 1990b Inner morphology of the arrester-system in the damselfly *Erythromma najas* Hansemann (Zygoptera, Coenagrionidae). *Vestnik Zool.* **N6**, 59–62. (In Russian.)
- Gorb, S. N. 1990c Morphology of the head fixation system in calopterygoid damselflies (Odonata, Zygoptera, Calopterygoidea). *Zool. Zh.* **69**, 37–45. (In Russian.)
- Gorb, S. N. 1991a Sensilla in the odonate arrester system (Odonata). *Vestn. Zool.* **N1**, 61–68. (In Russian.)
- Gorb, S. N. 1991b Flight reflexes connected to the head fixation system in dragonflies (Odonata). *Zh. Evol. Bioch. Physiol.* **27**, 46–51. (In Russian.)
- Gorb, S. N. 1993 The skeleton–muscle organization of the head-fixation system in odonates and its evolutionary implications: a comparative study. *Petalura* **1**, 3–17.
- Gorb, S. N. 1995 The dragonfly head arrester: a sensory organ connected to flight reflexes. In *Proceedings of the 23rd Göttingen Neurobiology Conference*, vol. 2, p. 193. Stuttgart and New York: Georg Thieme Verlag.
- Gorb, S. N. 1996a Initial stage of tandem contact in *Platynemis pennipes* Pall. (Zygoptera; Platynemididae). *Odonatologica* **25**, 371–376.
- Gorb, S. N. 1996b Design of insect unguitractor apparatus. *J. Morphol.* **230**, 219–230.
- Gorb, S. N. 1997a Ultrastructural architecture of the microtrichia of the insect cuticle. *J. Morphol.* **234**, 1–10.
- Gorb, S. N. 1997b Porous channels in the cuticle of the head-arrester system in Odonata. *Microsc. Res. Techn.* **37**, 583–591.

- Gorb, S. N. 1997c Armoured membranes in Brachycera (Diptera). *J. Morphol.* **234**, 213–222.
- Hengstenberg, R. 1991 Gaze control in the blowfly *Calliphora*: a multisensory, two-stage integration process. *The Neurosciences* **3**, 19–29.
- Heymer, A. 1975 Der stammesgeschichtliche Aussagewert des Verhaltens der Libelle *Epallage fatime* Charp., 1840. *Z. Tierpsychol.* **37**, 163–181.
- Ilychev, V. D. (ed.) 1987 *Biological damage*. Moscow: Vysshaja Shkola. (In Russian.)
- Kiauta, B. 1968 Evolution of the chromosome complement in Odonata. *Entomol. Berichte*. **28**, 97–100.
- Liske, E. 1982 Proprioceptive control of head position and head movement in the praying mantis. *Naturwissenschaften* **69**, 452–453.
- Liske, E. 1984 Head movements of the praying mantis with particular reference to visual and proprioceptive information. *Int. Congr. Entomol. Proc.* **17**, 195.
- Liske, E. 1989 Neck hair plate sensilla of the praying mantis: central projections of the afferent neurones and their physiological responses to imposed head movement in the yaw plane. *J. Insect Physiol.* **35**, 677–687.
- Liske, E. & Davis, W. J. 1986 Behavioral suppression of head grooming in the male praying mantis during mating. *Naturwissenschaften* **73**, 333–334.
- Liske, E. & Mohren, W. 1984 Saccadic head movements of the praying mantis, with particular reference to visual and proprioceptive information. *Physiol. Entomol.* **9**, 29–38.
- Martynov, A. V. 1924 Wing venation and tracheation in Odonata and Ephemeroptera. *Rus. Entomol. Obozr.* **18**, 145–174. (In Russian.)
- Mittelstaedt, H. 1950 Physiologie des Gleichgewichtsinnes bei fliegenden Libellen. *Z. Vergl. Physiol.* **32**, 442–463.
- Olberg, R. M. 1978 Visual and multimodal interneurons in dragonflies. *Diss. Abstr. Int. B Sci. Eng.* **39**, 2175.
- Olberg, R. M. 1981 Object- and self-movement detectors in the ventral nerve cord of the dragonfly. *J. Comp. Physiol. A* **141**, 327–334.
- Olberg, R. M. & Pinter, R. B. 1990 The effect of mean luminance on the size selectivity of identified target interneurons in the dragonfly. *J. Comp. Physiol. A* **166**, 851–856.
- Olesen, J. 1972 The hydraulic mechanism of labial extension and jet propulsion in dragonfly nymph. *J. Comp. Physiol.* **81**, 53–56.
- Parry, D. A. 1983 Labial extension in the dragonfly larva *Anax imperator*. *J. Exp. Biol.* **107**, 495–499.
- Pfau, H. K. 1971 Struktur und Function des sekundären Kopulationsapparates der Odonaten (Insecta; Palaeoptera) ihre Wandlung in der Stammesgeschichte und Bedeutung für die adaptive Einfaltung der Ordnung. *Z. Morphol. Tiere*. **70**, 281–371.
- Pfau, H. K. 1986 Untersuchungen zur Konstruktion, Funktion und Evolution des Flugapparates der Libellen (Insecta; Odonata). *Tijdsch. Entomol.* **129**, 35–123.
- Pfau, H. K. 1991 Contributions of functional morphology to the phylogenetic systematics of Odonata. *Adv. Odonatol.* **5**, 109–141.
- Popham, E. J. & Bevans, E. 1979 Functional morphology of the feeding apparatus in larval and adult *Aeshna juncea* L. (Anisoptera; Aeshnidae). *Odonatologica* **8**, 301–318.
- Pringle, J. 1963 *Insect flight*. Moscow: Izd. Inostr. Literat. (In Russian.)
- Pritykina, L. N. 1980 Odonatoptera. *Trudy PLN AN SSSR* **178**, 128–134. (In Russian.)
- Sandeman, D. & Markl, H. 1980 Head movements in flies (*Calliphora*) produced by deflexion of the halteres. *J. Exp. Biol.* **85**, 43–60.
- Snodgrass, R. E. 1909 The thorax of insects and the articulations of the wings. *Proc. US Nat. Mus. Wash.* **36**, 511–595.
- Steinmann, H. 1967 A study of the cephalic measurement values of the species of European Odonata families. *Dtsch. Entomol. Z.* **4**, 265–275.
- Strausfeld, N. J., Seyan, H. S. & Milde, J. J. 1987 The neck motor system of the fly *Calliphora erythrocephala*. Muscles and motor neurons. *J. Comp. Physiol. A* **160**, 205–224.
- Tanaka, Y. & Hisada, M. 1980 The hydraulic mechanism of the predatory strike in dragonfly larvae. *J. Exp. Biol.* **88**, 1–19.
- Tillyard, R. J. 1917 *The biology of dragonflies* (Odonata or Paraneuroptera). Cambridge University Press.
- Tillyard, R. J. 1928 The evolution of the order Odonata. In *Proceedings of the Fourth International Congress of Entomology*, pp. 543–545. Hamburg.
- Wildermuth, H. 1984 Drei aussergewöhnliche Beobachtungen zum Fortpflanzungsverhalten der Libellen. *Mitt. Entomol. Ges. Basel* **34**, 121–129.
- Zalessky, Yu. M. 1932 About the wing venation in dragonflies and their phylogeny. *Izvestija AN SSSR. Otd. Matem. Estestv. Nauk.* **8**, 713–733. (In Russian.)

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.