

SPINES ON THE WING VEINS IN ODONATA. 3. THE VEIN EDGE *

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The wing edge veins have a double row of Sc-type (keel-shaped apse) spines, like those on the convex side of the internal wing veins. On the trailing edge the apse of the spines is partially rotated longitudinally : this does not occur in Coenagrionidae and Libelluloidea but does in all other groups (including Anisozygoptera), suggesting that it is a very old character. In Anisoptera, with the exception of Libelluloidea, the apse rotation is complete and the keel separated, resulting in a shape similar to an upside-down heart ("heart-shaped spine"). It is not clear, however, if this represents a convergence between different groups of Anisoptera or if this is a true synapomorphism. The density of the edge spines in Zygoptera (densest at the apex) differs from that in both Anisozygoptera and Anisoptera. The relative density of the two rows of spines also differs between the suborders. Instead, a marked thinning out of the upper row in proximity to the forewing anal field is common in all three suborders. The spines on the lower row tend to be longer than normal, as are those on the inner veins of the cubito-anal field. The different shape and density of the spines on the hind and fore wings modify the air flow existing from the trailing edge, modifications which could be due to different requirements of both wings during flight.

INTRODUCTION

The study of the spines on the wing edge of Odonata is the last in a series of studies covering the morphology, systematics and function of the internal

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wing vein spines (D'ANDREA & CARFI, 1988, 1989), sexual differentiation in distribution (D'ANDREA & CARFI, 1990), and importance in wing aerodynamics (D'ANDREA & CARFI, 1991). The above research has revealed aspects regarding subfamilies which are to be the subject of future studies.

While the internal wing vein spines had not been studied in detail prior to our above-mentioned research, those on the wing edge had been observed by HERTEL (1966). He suggested that the spines act as turbulators, an hypothesis which NEWMAN *et al.* (1977) verified by testing the model of an *Aeshna interrupta* wing. The spines were seen to create artificial turbulence in the boundary layer thus increasing lift at the speed typical of Odonata flight. As this was verified in stationary flight, the air currents were exclusively transversal. Only the function of a single wing was investigated. Like the internal wing spines, nothing or almost nothing was known about their zoological characteristics.

MATERIAL AND METHODS

The morphology and size of the wing edge vein spines were defined under the SEM, and their density and distribution with a stereo-microscope, subdividing the wing edge into the following 8 zones: 1) first antenodals, 2) las antenodals, 3) first post-nodals, 4) Pt, 5) apex, 6) proximal to R3, 7) proximal to MA, and 8) proximal to 1A. The density was calculated in sectors 4 mm long and averaged on 1 mm, except for the apical zone where the count was made directly on 1 mm sectors due to the marked curvature of the wing edge. The species studied quantitatively are listed in Table II, while those examined qualitatively are mentioned in the text. All the specimens belong to 'La Specola' Zoological Museum of Florence University, Italy.

ABBREVIATIONS

The vein nomenclature is according to TILLYARD & FRASER, 1938-40. The spine nomenclature (D'ANDREA & CARFI, 1988, 1989) is: 'L' (= long) needle-shaped spines found in the main vein 'valleys' and on the underside of the cross veins, 'Sc' (= short carinate) spines similar to rose thorns or saw teeth, with a posterior abside and keel found on the main vein 'crests' and upperside of the cross veins in Zygoptera, and 'Se' (= short elongate) Sc-derived spines very similar to L spines on the upper side of the cross veins in Anisozygoptera and Anisoptera.

MORPHOLOGY

ZYGOPTERA

The leading wing edge has two parallel rows of Sc spines (Fig. 1), one on the upper and one on the antero-lower surface, so that in section the vein is concave with a central gutter between the two rows of spines. The axillary base differs from this model in being broadened (Fig. 1A): the anterior lamina is projected frontally in the forewing, and is curved — slightly or markedly —

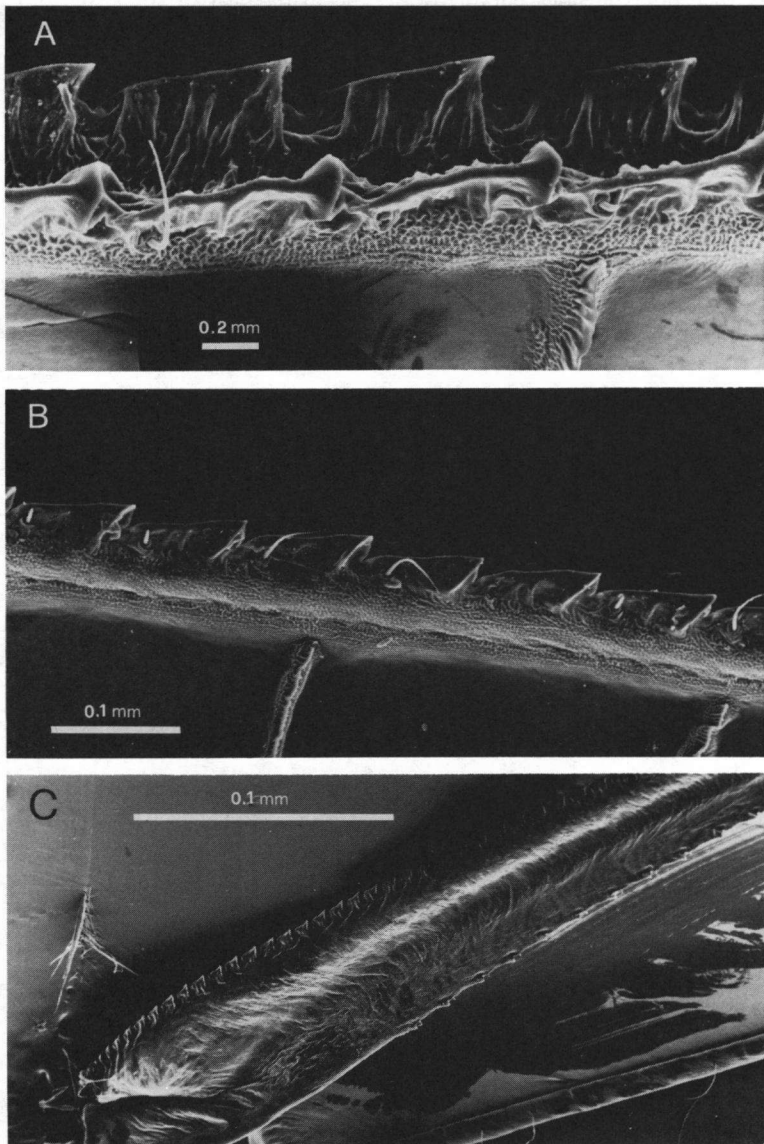


Fig. 1. Edge spines from the wing base (A) to the nodus (B) and at the Pt (C) in *Calopteryx haemorrhoidalis*.

downward in the hindwing, appearing in profile like an italic S. On both edges the spines absides curve toward the distal part of the wing, aimed at a point between the R2 and IR2 veins which shifts slightly in the species we observed but which does not, apparently, have any systematic significance. In this zone the two rows of converging spines give origin to one or more crests without any or else with double absides, i.e., in contraposition and oriented in opposite directions. This arrangement allows pinpointing the 'morphological apex' of the wing with a relative degree of accuracy (Fig. 2A).

As on the internal veins, the great variability of the spines along the edge veins makes it practically impossible to establish a representative size for these. However, Table I reports the mean size and distance of the spines in five species of Odonata.

Table I

Mean values (μm) (1 male per species) of the size (abside height) and distance (between abside vertexes) of the forewing edge spines in five Odonata species.
U, upper row of spines ; L ; lower row of spines ; s, size ; d, distance.

		base nodus	nodus Pt	Pt apex	R2- IR3	Cup- A1
<i>Calopteryx haemorrhoidalis</i>						
U	s	36	35	28	38	14
	d	107	58	61	64	114
L	s	36	38	28	41	25
	d	94	61	62	63	93
<i>Lestes viridis</i>						
U	s	16	20	14	17	10
	d	213	104	61	92	321
L	s	19	33	20	17	19
	d	145	112	74	130	207
<i>Ceriatrion tenellum</i>						
U	s	19	20	21	19	12
	d	85	86	67	89	121
L	s	23	25	26	25	19
	d	118	88	83	72	79
<i>Anax imperator</i>						
U	s	38	33	22	38	21
	d	98	160	196	220	371
L	s	61	57	20	33	32
	d	109	133	177	221	214
<i>Sympetrum fonscolombei</i>						
U	s	31	30	27	25	11
	d	190	174	138	95	233
L	s	27	33	29	37	24
	d	139	114	63	91	120

The spines are morphologically more homogenous on the leading edge from the base to the apex (as defined above) as can be seen by comparing (Fig. 1) the base (A), nodus (B) and Pt (C) in *Calopteryx haemorrhoidalis*. At the axillary base, instead, the spines on the upper row resemble simple notches with little or no keel. They also begin 1-2 mm from the base whereas those on the lower row begin right at the vein base.

The spines of the trailing edge are less regular, with more indented and longer crests and no resemblance to the "serrated" spines typical of the leading edge (Fig. 2B). The spines often belend to from a sort of double serpentine crest running along the edge.

The situation is more complicated in the cubito-anal field. In the ancient groups (Calopterygoidea, Lestoidea) the abside is rotated around its axis so that it is parallel to the edge vein (Fig. 2C, 3A), giving rise to an 'intermediate' shape which — in Anisozygoptera and Anisoptera — is further modified into the "heart-shaped" spines described below. No such shape has been observed in Coenagrionoidea, in which the posterior crest of the spines diminishes giving them a more or less spur like appearance, particularly on the lower row of the forewing (Fig. 3B). Furthermore, in Coenagrionoidea, the upper row of cubito-anal spines on the forewing edge is so thinned out as to make the vein appear smooth, whereas nothing of the sort — or at least nothing in such a marked form — happens on the hindwing.

Other species studied from this point of view, aside from those listed in Table II, are : *Chalopteryx rutilans* (Rambur, 1842) (1 male, Brazil) (Polythorinae) ; *Calopteryx virgo* (L., 1758) (2 males, 1 female, Italy) (Calopteryginae) ; *Lestes dryas* Kirby, 1890 (1 male, 1 female, Italy), *Lestes barbarus* (F., 1798) (1 male, 1 female, Italy) (Lestinae) ; *Pyrrhosoma nymphula* (Sulzer, 1776) (2 males, 1 female, Italy) (Coenagrioninae). None of these differ substantially from the above described model. No sexual differences were observed.

ANISOPTERA

Like Zygoptera the leading wing edge veins of Anisoptera have Sc spines which form two saw-toothed crests from the base to the nodus. Above, the vein base is smooth for 1-2 mm while below spines appear immediately..

Unlike Zygoptera, as is known, Anisoptera present a third, lower crest from the wing nodus to the apex, giving the edge section a T-shape (Fig. 3C). The crest is spineless except in some species of Gomphidae, Neopetaliidae, Aeschnidae, Corduleagastridae and Libellulidae. But within these families the distribution of the spines — which at times are marked, at times barely visible, often present only near the Pt — is not at all clear : not all species, even within the same genus, have them. We found, for example, that *Orithetrum cancellatum* has spines but *O. brunneum* does not, that *Gomphus vulgatissimus*

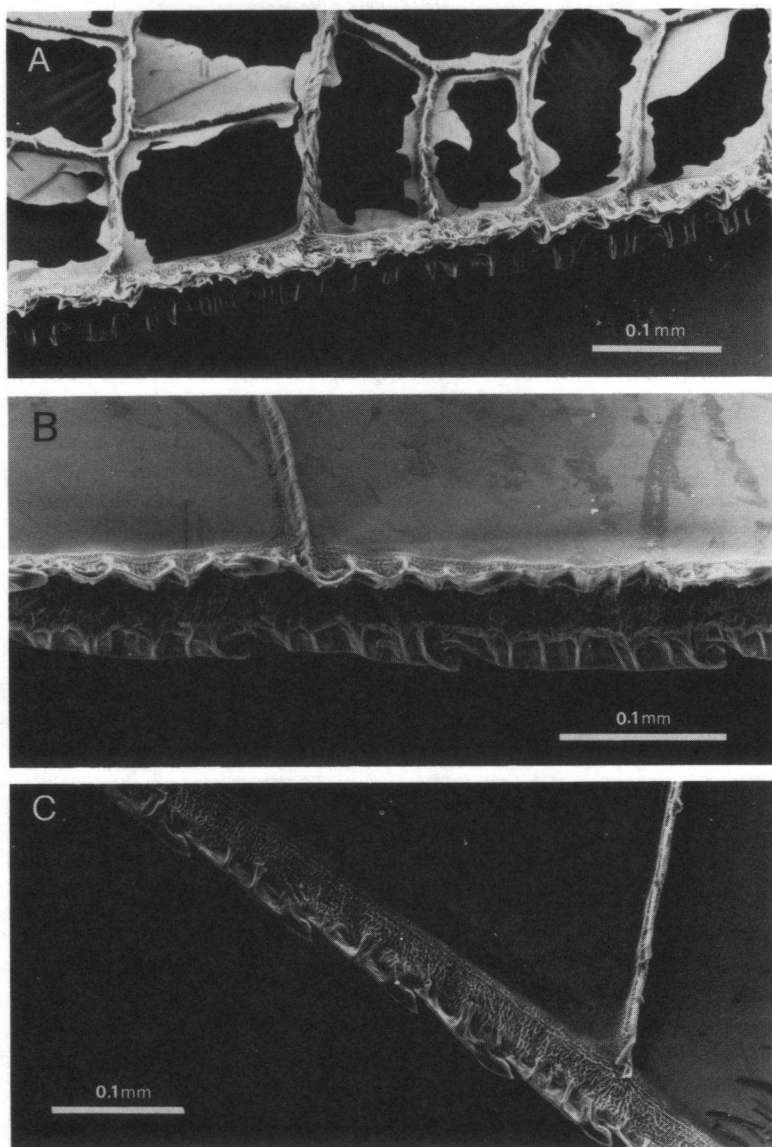


Fig. 2. Edge spines in proximity to R3 (A), MA (B) and A1 (C) in *Calopteryx haemorrhoidalis*.

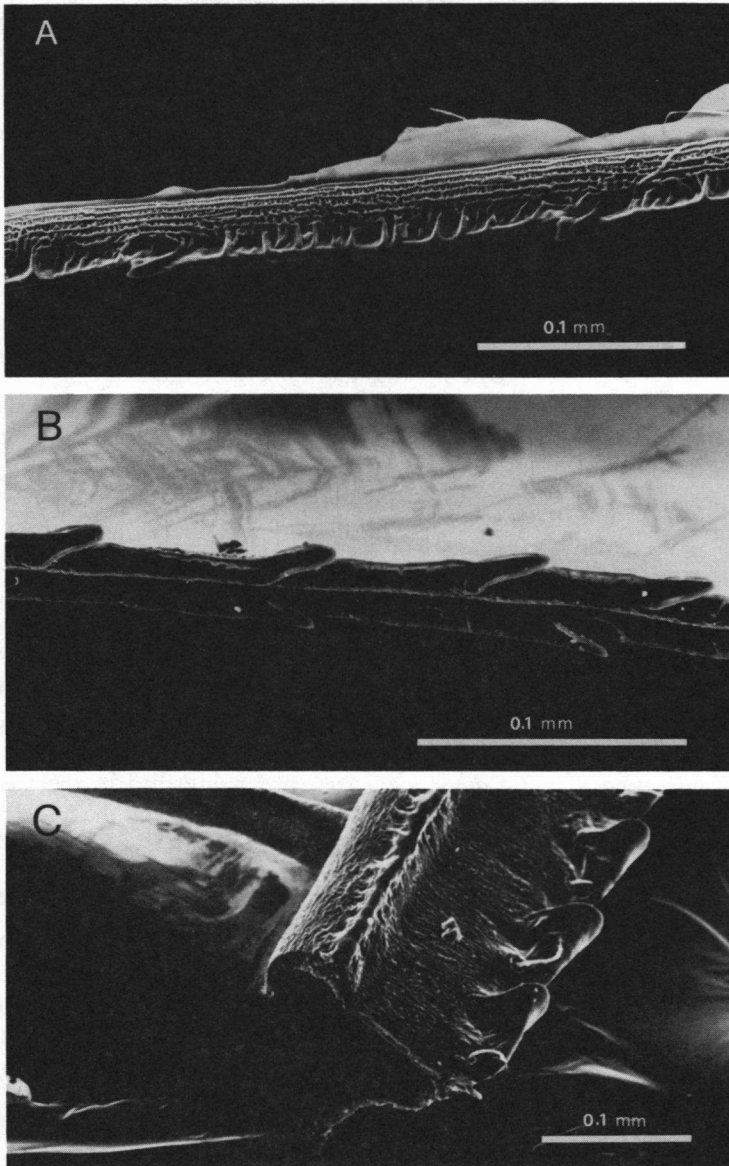


Fig. 3. Edge spines in proximity to A1 in *Lestes viridis* (A) and *Ceriagrion tenellum* (B); edge vein section between the nodus and Pt in *Libellula quadrimaculata* (C).

has only a few while *G. flavipes* has many, that *Gynacantha sextans* and *G. bullata* have none while *G. nervosa* has a few, that *Cordulegaster bidentatus* and *C. boltoni* are smooth while *C. principes* has a few spines near the Pt. The phenomenon obviously requires further investigation which might very well reveal that spines are present in all genera, in species as yet not observed by us.

The axillary base, as in Zygoptera, is broad and provided with very small spines above (beginning 1-2 mm from the vein origin) and dense large spines on the anterior lamina. In cross-section the axillary base is roughly horizontal in the forewing and curved slightly downward in the hindwing, creating an italic 'S'-shaped profile. The vein widens at the Pt also, increasing the frontal section.

The trailing edge is provided with Sc spines, albeit highly modified, which differ notably from the preceding ones and undergo a gradual transformation beginning at the apex. This starts with 'normal' Sc spines which rotate their abside longitudinally (Fig. 4A) to form an initial anterior notch (Fig. 4B) and then a second posterior one between the crest and the abside (Fig. 4C), forming a sort of upside-down heart. These spines were first described as 'ace of spades-shaped' spines due to a sort of 'tail' that appears in some subfamilies (D'ANDREA & CARFI, 1990) but we now propose the name 'heart-shaped' spines as being more elegant and appropriate. In the older families of Anisoptera (Gomphidae, Petaluridae, Neopetalidae, Aeshnidae, and Cordulegastridae) the crest is very indented but separate from the abside (the 'heart') in the median part of the trailing edge. More or less marked differences appear in the shape of the 'heart': it is relatively short and broad in *Gynacantha*, well-balanced in *Anax* and *Aeshna*, rather pointed in *Brachytron*, and fairly small and rounded in *Cordulegaster*. The crest is attached to the abside in the remaining parts of the trailing edge towards the apex and the base (Fig. 5). This is also the only form encountered in the more recent families (Corduliidae and Libellulidae) as well as in some Calopterygoidea and Lestoidea.

Like Zygoptera, on the forewing the lower spines in anal field can be rather long, particularly in Libellulidae, while the upper ones show the same reduction in number and size (Table II).

In addition to those in Table II the following species were also studied (the presence of spines on the lower surface in the nodus-Pt tract is indicated by a plus (+) sign after the species name): *Hypopetalia petilens* (McLachlan, 1870) (+) (1 male, Chile), *Gomphidia quarrei* Schouteden, 1934 (1 male, Zaire) (Gomphinae), *Gomphus vulgatissimus* (L., 1758) (+) (1 male, 1 female, Italy), *Gomphus flavipes* (Charpentier, 1825) (+) (1 male, 1 female, Italy), (Gomphinae); *Gynacantha bullata* Kasch, 1891 (1 male, Zaire), *G. nervosa* Rambur, 1842 (+) (1 male, 1 female, USA), *G. sextans* McLachlan, 1896 (1 male, Zaire), *Heliaeshna libyana* (Fraser, 1928) (1 male, R. P. Congo), *H. fuliginosa* Krasch,

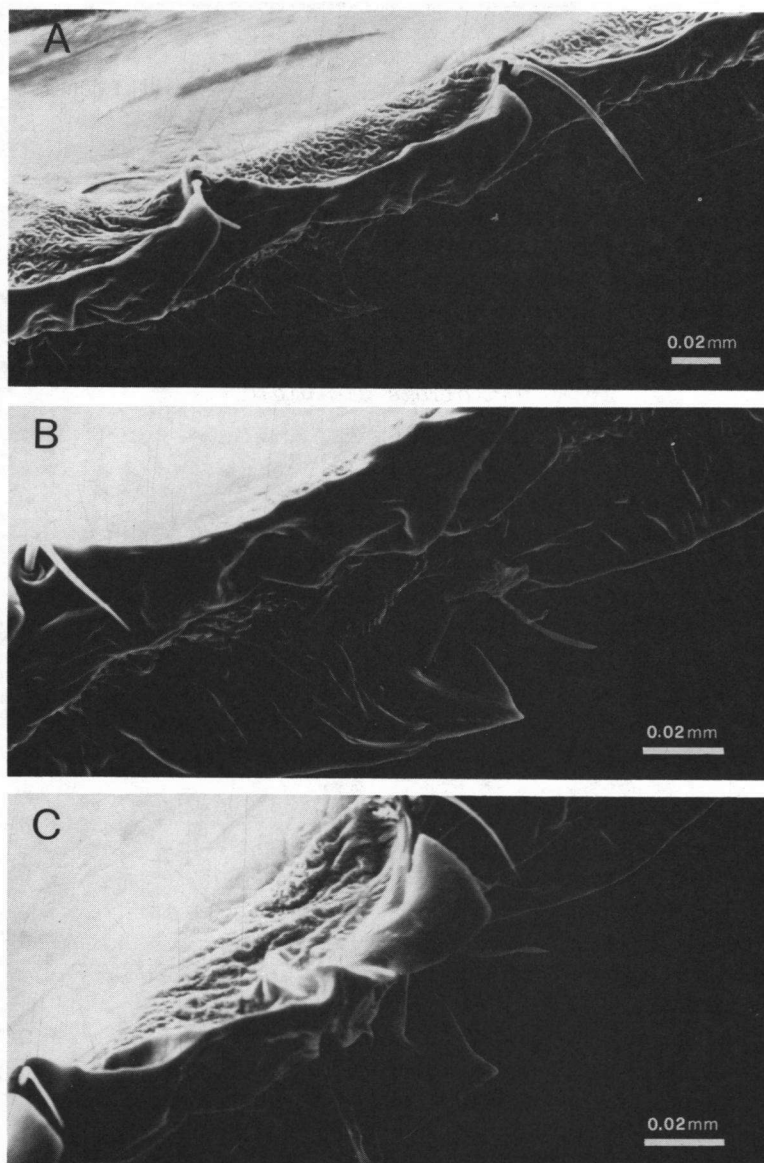


Fig. 4. Formation stages of the 'heart-shaped' spines.

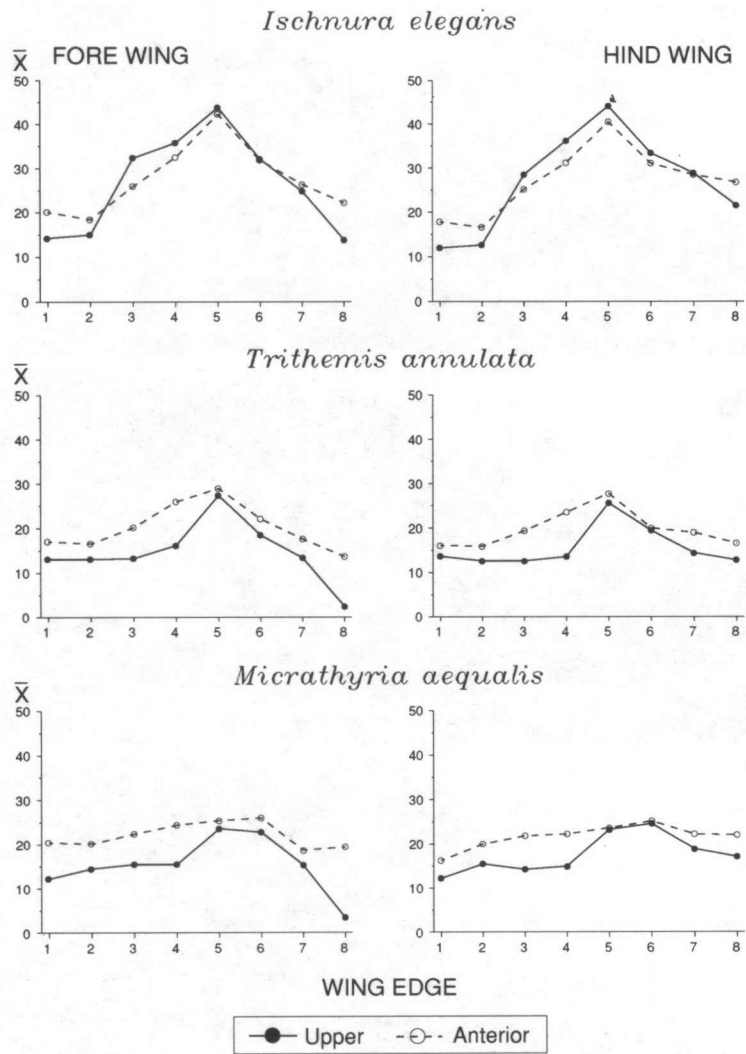


Fig. 5. Edge spine density in three sample species. Data from Table III.

1893 (1 male, R. P. Congo), *Aeshna rileyi* Calvert, 1892 (1 male, Ethiopia), *Anaciaesha isosceles* (Müller, 1767) (1 male, 1 female, Italy), *Coryphaesha virens* (Rambur, 1842) (1 male, Cuba), *Anax guttatus* (Burmeister, 1839) (1 male, Phillipines), *A. parthenope* (Sélys, 1839) (1 male, 1 female, Italy), *A. strenuus* Hagen, 1867, *A. tumorifer* McLachlan, 1883 (1 male, Somalia) (Aeshninae); *Boyeria irene* (Fonscolombe, 1838) (1 male, 1 female, Italy) (Brachitroninae); *Cordulegaster bidentatus* Sélys, 1843 (1 male, 1 female, Italy), *C. princeps* Morton, 1915 (+) (1 male, Morocco) (Cordulegastrinae); *Cordulia aenea* (L., 1758) (1 male, 1 female, Italy), *Epicordulia princeps* (Hagen, 1861) (1 male, Canada) (Corduliinae); *Macromia splendens* (Pictet, 1843) (1 male, France); *M. schoutedeni* Fraser, 1954 (1 male, Zaire) (Macro-miinae); *Allorhizuca preussi* Karsch, 1891 (+) (1 male, R. P. Congo) (Tetra-themistinae); *Chalcostephia flavifrons* Kirby, 1889 (1 male, Zaire), *Eleuthe-mis buettikoferi* Ris, 1910 (1 male, R. P. Congo), *Hemistigma affinis* (Rambur, 1842) (1 male, Madagascar), *Micrathyria aequalis* (Hagen, 1861) (+) (1 male, Cuba), *M. dissocians* Calvert, 1906 (1 male, Cuba) (Brachydiplacinae); *Celi-themis eponina* (Drury, 1773) (1 male, USA) (Leucorrhiniinae); *Hadrothemis defecta* (Karsch, 1891) (1 male, R. P. Congo), *H. infesta* (Karsch, 1891) (1 male, Somalia), *Orthetrum brunneum* (Fonscolombe, 1837) (1 male, 1 female, Italy), *O. coerulescens* (F., 1798) (+) (1 male, 1 female, Italy), (Libellulinae); *Acisoma panorpoides ascalafoides* Rambur, 1842 (+) (1 male, R. P. Congo), *A. tri-fidum* Kirby, 1889 (+) (1 male, 1 female, R. P. Congo), *Brachythemis lacustris* (Kirby, 1889) (1 male, Somalia), *Diplacodes lefebvrei* (Rambur, 1842) (1 male, 1 female, Somalia), *Erythemis plebeja* (Burmeister, 1839) (1 male, Cuba), *Sympetrum fonscolombeii* (Sélys, 1840) (1 male, 1 female, Italy), *S. meridionale* (Sélys, 1841) (1 male, 1 female, Italy), *S. striolatum* (Charpetier, 1840) (1 male, 1 female, Italy), (Sympetrinae); *Dythemis fugax* Hagen, 1861 (1 female, USA) (Trithemistinae); *Miathyria marcella* (Sélys, 1857) (1 male, Cuba) (Trameinae), and *Aethriamanta rezia* Kirby, 1889 (1 male, R. P. Congo) (Urothemistinae). The 'heart-shaped' spines on the hindwing edge of Gynacanthini are unique in that they are broader and have a distinct 'stem' which causes them to look very much like the spade symbol of playing cards. However, none of these species differ substantially from the model of distribution described above. No sexual differences were observed.

ANISOZYGOPTERA

In *Epiophlebia superstes* (Sélys, 1889) the spine shape and distribution and appearance of the edge veins in section are comparable to that observed in Anisoptera. Instead of being typically 'heart-shaped' the spines on the hindwing edge have the intermediate form found in all the Anisoptera and older Zygoptera families.

Table II
Distribution of the edge spines in Odonata.

	1	2	3	4	5	6	7	8
ZYGOPTERA								
Calopteryidae								
<i>Calopteryx haemorrhoidalis</i>	29	27	33	37	43	36	19	18
(Vander Linden, 1825)	31	25	27	26	36	30	19	21
♂, Italy	19	25	28	32	31	27	21	21
	22	26	28	27	37	26	23	23
<i>Hetaerina rosa</i>	25	20	31	38	40	27	15	16
Sélys, 1853	31	28	31	37	36	28	14	23
♂, Ecuador	12	15	31	39	43	26	20	20
	22	22	30	35	40	37	29	25
<i>Phaon iridipennis</i>	26	22	32	30	38	25	22	13
(Burmeister, 1839)	26	25	31	29	48	32	23	32
♂, Somalia	20	19	27	28	36	31	24	22
	22	19	25	27	42	34	26	24
Chlorocyphidae								
<i>Chlorocypha selysi</i>	23	35	38	40	39	30	16	23
Karsch, 1899	35	33	40	41	40	31	28	32
♂, Zaire	19	30	35	32	42	33	32	29
	31	29	31	40	44	25	28	31
Lestidae								
Lestinae								
<i>Lestes barbarus</i>	8	8	13	18	24	20	12	8
(F., 1798)	17	12	15	19	25	18	10	6
♀, Italy	9	9	10	19	21	16	14	8
	14	12	12	20	24	15	16	12
Sympecmatinae								
<i>Austrolestes</i> sp.	9	10	11	12	17	16	10	8
(Tillyard, 1913)	10	11	11	13	14	11	9	7
♀, Australia	7	8	10	11	19	16	10	10
	8	10	14	14	14	6	9	9
<i>Sympecma fusca</i>	12	13	12	16	30	25	12	7
Vander Linden, 1823)	17	13	15	18	27	18	11	11
♀, Italy	10	11	10	15	23	15	13	17
	15	12	16	17	23	22	19	14
Megapodagrionidae								
<i>Hypolestes trinitatis</i>	8	14	20	28	34	30	16	13
(Gundlach, 1888)	15	18	25	28	29	30	22	18
♂, Cuba								

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	1	2	3	4	5	6	7	8
Pseudostigmatidae								
<i>Mecistogaster lucretia</i>	10	13	14	24	20	30	18	5
(Drury, 1773)	12	14	11	16	17	?	?	11
♂, Surinam	5	7	13	10	17	27	24	13
	11	11	11	20	20	17	14	15
<i>Megaloprepus caerulatus</i>	8	9	14	21	17	19	12	4
(Drury, 1782)	11	13	12	31	18	18	10	10
♂, Colombia	6	6	11	21	21	19	15	11
	8	10	10	15	14	14	12	10
Protoneuridae								
<i>Neoneura carnatica</i>	11	15	24	28	38	32	26	11
Sélys, 1886	20	21	22	24	29	28	18	16
♂, Cuba	8	12	24	28	36	31	26	25
	19	19	20	24	31	23	21	24
Platycnemididae								
<i>Platycnemis pennipes</i>	12	13	18	26	32	26	17	9
(Pallas, 1771)	19	15	18	25	34	25	20	16
♂, Italy	12	11	19	25	33	26	15	13
	16	16	18	23	38	26	23	18
<i>Risio cnemis incis</i>	10	12	16	22	35	33	24	8
Kimmins, 1936	16	15	18	23	34	33	21	12
♂, Philippines	8	5	14	24	32	30	25	14
	12	10	13	16	31	22	19	13
Coenagrionidae								
Arginae								
<i>Argia oculata</i>	9	13	26	27	40	33	20	10
Hagen, 1865	16	21	24	26	35	32	19	18
♂, Guyana	7	9	19	25	36	30	22	16
	14	15	20	23	30	24	17	16
Coenagrioninae								
<i>Cercion lindeni</i>	19	17	22	32	37	32	24	12
(Sélys, 1848)	21	16	19	25	38	29	29	18
♂, Italy	13	14	19	29	36	35	28	18
	15	12	19	21	32	27	27	22
<i>Coenagrion mercuriale</i>	14	11	20	27	30	28	20	9
<i>castellani</i>								
Roberts, 1948	20	18	18	22	28	30	19	19
♀, Italy	13	13	17	20	26	27	20	12
	14	18	20	25	25	27	21	19
<i>Erythromma viridulum</i>	13	12	24	28	26	35	17	10
Charpentier, 1840	22	20	21	25	40	34	18	15
♂, Italy	14	16	27	29	36	30	23	15
	15	16	22	27	35	30	23	20

	1	2	3	4	5	6	7	8
Ischnurinae								
<i>Enallagma cardenium</i>	21	16	32	37	45	35	24	13
Sély, 1876	28	24	32	34	52	31	20	22
♂, Cuba	14	15	31	35	50	37	34	25
	22	20	29	31	52	31	21	24
Pseudagrioninae								
<i>Ceriagrion annulatum</i>	21	18	31	34	41	37	28	14
Fraser, 1955	23	20	27	27	36	31	23	20
♀, Rep. Pop. Congo	13	15	28	32	39	32	26	22
	20	16	24	28	32	25	23	22
<i>Ceriagrion corallinum</i>	18	17	28	32	46	36	31	12
Campion, 1914	22	20	26	30	35	27	25	20
♂, Rep. Pop. Congo	13	16	26	31	40	32	27	20
	18	16	29	26	27	30	25	23
<i>Ceriagrion glabrum</i>	15	19	28	36	50	41	19	12
(Burmeister, 1839)	23	20	24	29	45	36	24	20
♂, Somalia	13	17	27	34	49	31	24	20
	18	19	22	31	42	29	23	25
<i>Pseudagrion melanicterum</i>	13	14	27	34	41	37	30	14
Sély, 1876	21	20	24	30	38	30	26	18
♀, Sierra Leone	10	12	25	32	43	35	31	22
	18	15	24	28	38	30	24	25
<i>Telebasis dominicana</i>	14	16	26	32	34	32	16	7
(Sély, 1857)	21	17	23	27	28	28	21	21
♂, Cuba	11	13	24	30	36	30	29	26
	15	16	21	24	32	24	23	26
ANISOZYGOPTERA								
Epiophlebiidae								
<i>Epiophlebia superstes</i>	8	5	7	5	11	12	9	7
(Sély, 1889)	16	13	14	14	13	10	8	6
♂, Japan	4	7	6	7	14	10	7	6
	10	9	9	11	12	13	10	9
ANISOPTERA								
Gomphidae								
Onychogomphinae								
<i>Onychogomphus</i>	15	14	15	15	15	21	16	9
<i>forcipatus</i>	22	15	20	18	18	23	22	19
(L., 1758)				15				
♂, Italy	13	12	17	16	14	18	19	13
	20	13	18	19	16	23	20	21
				7				
Gomphoidinae								
<i>Progomphus zonatus</i>	10	10	12	12	11	17	14	1
Hagen, 1854	16	16	15	17	15	19	16	15
♂, Mexico	14	11	13	11	10	18	15	13
	18	17	15	18	13	22	19	17

	1	2	3	4	5	6	7	8
Lindeninae								
<i>Ictinogomphus ferox</i>	11	8	10	10	10	15	9	12
(Rambur, 1842)	14	15	13	18	12	18	14	25
♀, Somalia	11	10	9	11	12	14	12	9
	13	15	12	17	11	23	17	15
<i>Lindenia tetraphylla</i>	11	8	7	8	9	9	8	14
(Vander Linden, 1825)	14	12	12	17	13	17	16	14
♂, Yugoslavia	11	8	9	9	10	12	10	11
	11	10	8	12	12	17	14	13
Aeshnidae								
Aeshninae								
<i>Aeshna affinis</i>	9	12	10	11	8	9	8	7
(Vander Linden, 1823)	14	12	12	14	11	9	8	9
♀, Italy	9	11	12	10	7	10	10	9
	13	11	10	13	10	10	10	10
<i>Aeshna cyanea</i>	15	13	16	16	9	13	13	12
(Müller, 1764)	25	22	24	26	18	14	16	15
♂, Italy	10	14	14	15	9	13	12	12
	22	18	22	23	14	13	14	17
<i>Aeshna mixta</i>	10	15	14	13	11	12	9	13
(Latreille, 1805)	14	18	15	18	11	13	14	13
♀, Italy	8	13	9	13	9	14	9	8
	14	16	14	20	13	15	12	14
<i>Anax imperator</i>	11	14	14	13	13	9	12	18
Leach, 1815	19	14	18	17	17	11	12	10
♂, Italy	13	9	13	10	9	13	10	15
	14	13	14	15	15	15	14	15
<i>Heliaeshna lanceolata</i>	13	8	11	10	9	12	10	9
Le Roi, 1915	24	21	22	24	12	13	11	12
♂, Zaire	11	9	10	7	8	10	9	11
	19	17	21	19	12	13	10	14
<i>Gynacantha cylindrata</i>	15	12	12	9	13	14	10	10
Karsch, 1891	25	27	27	25	17	17	15	17
♂, Zaire	9	10	10	9	13	13	12	14
	18	22	23	27	14	17	14	18
<i>Gynacantha manderica</i>	15	10	15	13	9	19	12	10
Grünberg, 1902	24	21	22	23	10	20	17	15
♀, Somalia	5	11	11	11	11	18	15	11
	16	15	16	20	15	20	16	14
Brachytroninae								
<i>Boyeria irene</i>	9	13	16	14	12	13	11	7
(Fonscolombe, 1838)	18	15	17	20	12	17	13	13
♂, Italy	7	11	14	12	10	13	11	13
	12	14	19	17	14	16	14	17

	1	2	3	4	5	6	7	8
<i>Brachytron pratense</i>	10	11	13	9	8	8	7	8
(Müller, 1764)	20	19	20	19	13	12	11	11
♂, Italy	12	10	10	10	8	9	9	10
	15	19	19	17	14	14	12	14
Neopetaliidae								
<i>Phyllopetalia apicalis</i>	9	8	9	9	10	9	5	9
Sélys, 1857	10	12	12	13	11	11	9	10
♂, Chile	9	11	10	12	9	13	11	8
	8	11	10	12	9	13	11	8
Cordulegastridae								
<i>Cordulegastrinae</i>								
<i>Cordulegaster boltonii</i>	6	5	7	9	11	9	0	3
(Donovan, 1807)	13	14	16	15	12	13	10	7
♂, Italy	5	8	8	9	16	10	7	8
	13	13	13	15	18	12	10	10
Corduliidae								
<i>Corduliinae</i>								
<i>Cordulia aenea</i>	14	15	14	13	14	9	10	3
(L., 1758)	21	18	17	19	16	12	13	16
♀, Italy	15	16	17	11	12	12	11	16
	17	18	17	19	16	13	20	19
<i>Hemicordulia mindana</i>	11	20	20	21	15	13	14	2
Needham & Gyger, 1937	36	44	38	43	24	19	19	19
♀, Philippine	14	18	19	23	19	17	16	15
	30	32	33	41	23	27	23	23
<i>Somatochlora metallica</i>	17	14	16	14	15	14	7	10
<i>meridionalis</i>								
Nielsen, 1935	21	20	23	22	16	17	14	13
♂, Italy	12	9	14	15	14	14	9	10
	16	17	21	23	15	20	12	16
Gomphomacromiinae								
<i>Oxygastra curtisii</i>	15	15	17	18	10	18	8	11
(Dale, 1834)	21	22	21	24	18	20	15	18
♂, Italy	13	16	16	23	14	14	13	14
	17	19	22	28	17	20	19	19
Libellulidae								
<i>Tetrathemistinae</i>								
<i>Micromcromia camerunica</i>	16	18	21	19	21	18	9	14
Karsch, 1890	24	29	29	32	36	27	21	15
♀, Congo	13	18	17	18	17	17	16	20
	23	26	27	29	34	22	18	19

	1	2	3	4	5	6	7	8
Leucorrhiniinae								
<i>Brachymesia herbida</i>	16	14	14	11	15	18	12	8
(Gundlach, 1889)	18	22	21	25	14	23	18	18
♂, Cuba	12	11	10	12	12	18	15	11
	17	19	18	26	17	22	20	16
<i>Leucorrhinia dubia</i>	11	14	12	15	12	18	11	5
(Vander Linden, 1825)	15	16	18	20	15	23	14	12
♂, Italy	11	10	13	14	11	19	15	14
	12	15	16	19	15	24	13	24
Libellulinae								
<i>Cannaphila insularis</i>	10	9	13	10	12	14	9	6
Kirby, 1889	15	13	18	18	13	17	14	15
♂, Cuba			9	8	7			
10	13	15	10	11	15	11	10	
	12	14	19	19	14	19	14	14
			6	8	4			
<i>Ladona fulva</i>	16	13	14	15	13	15	13	4
(Müller, 1764)	14	18	19	26	16	20	14	19
♂, Italy	15	13	13	12	13	17	14	14
	17	17	20	24	16	20	18	17
<i>Libellula depressa</i>	13	9	13	10	12	16	9	2
L., 1758	19	13	15	18	16	18	13	16
♀, Italy	12	9	10	11	15	15	13	16
	16	14	16	20	16	16	17	12
<i>Orthetrum cancellatum</i>	17	13	14	11	11	17	12	5
(L., 1758)	18	16	19	23	16	21	14	15
♀, Italy			6	9				
	11	12	13	10	8	16	14	14
	9	13	13	16	12	20	18	15
			4	9				
Sympetrinae								
<i>Brachythemis leucosticta</i>	14	15	19	15	12	20	15	5
(Burmeister, 1839)	13	15	16	15	13	26	20	16
♂, Zaire	13	15	16	15	13	26	20	16
	16	19	22	25	14	27	21	18
<i>Crocothemis erythraea</i>	10	13	12	13	12	15	13	18
(Brullé, 1832)	18	19	20	19	13	23	22	20
♂, Italy			11	15				
	8	12	9	12	11	10	9	14
	19	16	18	17	12	13	15	16
<i>Erythrodiplax umbrata</i>	13	12	10	11	14	18	15	11
(L., 1758)	17	13	12	19	15	21	18	17
♂, Cuba			7	9	9			
	11	9	9	9	12	17	14	17
	18	13	14	17	13	19	17	17
			10	10	11			

	1	2	3	4	5	6	7	8
<i>Philonomon luminans</i> (Karsch, 1893)	12 19	12 14	14 16	13 17	14 17	20 21	13 16	7 12
♂, Somalia			12 11	15				
	10 19	12 14	10 13	12 16	13 14	13 23	15 18	12 17
			9 11	11				
<i>Sympetrum sanguineum</i> (Müller, 1764)	13 16	12 15	12 15	14 24	16 20	22 29	15 19	5 17
♂, Italy	13 17	13 18	11 15	15 21	15 15	18 21	14 21	18 18
Tritheminae								
<i>Trithemis annulata</i> (P. de Beauvois, 1805)	15 16	13 18	14 19	16 30	15 18	14 20	8 17	3 15
♀, Italy	13 14	13 19	10 18	14 26	12 16	15 18	7 20	15 19
Palpopleurinae								
<i>Palpopleura lucia</i> (Drury, 1773)	13 17	13 16	14 17	12 18	14 13	13 17	11 19	9 19
♂, Zaire	10 16	12 18	11 16	12 19	10 13	14 20	13 19	12 14
Trameinae								
<i>Pantala flavescens</i> (F., 1798)	12 20	10 17	10 20	11 18	12 13	13 15	10 13	0 13
♀, Somalia			7 10					
	19 21	13 14	9 17	12 19	12 12	15 17	13 15	11 12
			6 8					
<i>Tauriphila australis</i> (Hagen, 1867)	10 15	10 14	12 15	12 18	13 11	17 18	10 14	5 13
♀, Cuba			4 4	13				
	12 10	10 11	11 12	12 16	11 12	19 19	12 17	7 12
			3 4	9				
<i>Tholymis tillarga</i> (F. 1798)	13 22	12 27	16 25	13 26	12 21	13 15	15 19	6 19
♂, Zaire			11 12					
	12 20	13 23	14 22	12 27	15 21	17 27	17 18	14 17
			9 8					
<i>Tramea cophysa</i> Hagen, 1867	6 15	10 13	8 10	11 13	10 12	11 15	10 10	4 8
♀, Guyana			6 10	10 9				
	12 14	8 9	10 10	11 13	10 12	13 14	10 12	6 10
			1 8	3				

	1	2	3	4	5	6	7	8
Urothemistinae								
<i>Macrodiplex cora</i>	13	15	13	13	14	9	8	5
(Brauer, 1868)	17	18	17	20	18	15	13	12
♂, Somalia				5				
	16	14	12	10	9	17	13	9
	14	15	14	16	14	18	18	14
			2					
<i>Selysiotemis nigra</i>	10	10	12	12	14	10	8	6
(Vander linden, 1825)	15	14	17	15	14	12	12	14
♂, Italy								
	12	12	11	13	12	14	11	6
	13	11	14	17	12	16	15	11

DISTRIBUTION

Table II lists all the Odonata species studied from a quantitative point of view and the density of their spines in the 8 edge zones selected for survey. The substantial similarity in trend to the individual graphs of each species examined (Zygoptera and Anisoptera) made it unnecessary to statistically examine a large number of conspecific specimens. However, to evaluate the degree of variability within each species, a reference curve was calculated for three randomly chosen sample specimens. The data on these species is reported in Table III and the relative graphs in Fig. 5. The standard deviation is relatively small but tend to increase near the apex which, due to the marked curvature of the edge vein in that point, could depend partly on an inaccuracy in counting the spines. Notably, the trend is different for Zygoptera and Anisoptera, as confirmed by the graphs regarding the other species extracted from the data of Table II. In Zygoptera, spine density increases greatly at the wing apex and in the surrounding zones, an increase visible to the naked eye. In Anisoptera, the increase in density is much more contained, often limited to the zone immediately behind the apex (R2-R3), and in some species can escape detection altogether. The spine density in *Epiophleba superstes* is somewhat similar to that in Anisoptera.

The spines are generally denser on the lower than on the upper rows, particularly in the base-nodus zone and, to a lesser degree, the cubito-anal fields. The only important exception is the apical zone in Zygoptera where the spines are denser on the upper rows (Table II), opposite to what occurs in Anisoptera.

Lastly, the spines are notably less dense on the upper row in the forewing anal field. As mentioned concerning the morphology, the reduction in size and number (due to an increase in the distance between the spines : Table I) can be so marked as to produce an almost completely smooth upper edge.

Table III

Mean spine density in three sample species of Odonata.
 Fw, forewing ; Hw, hindwing ; x, mean values ; on, standard deviation.

<i>Ischnura elegans</i> (8 ♀♀, 5 ♀♀ ; Italy)									
		1	2	3	4	5	6	7	8
fw	\bar{x}	14.2	15	32.4	35.8	43.8	32.1	24.8	13.8
	σ_n	2	1.3	3.3	2.8	4.5	3.2	3.2	2.1
	\bar{x}	20.1	18.4	26	32.5	42.3	31.8	26.4	22.2
	σ_n	2.2	2.4	2.5	3.9	4.5	4.3	2.6	3.1
hw	\bar{x}	12	12.6	28.5	36.2	44.1	33.4	28.9	21.5
	σ_n	2.1	1.6	2.9	2.3	4.5	2.7	2.8	2.8
	\bar{x}	17.8	16.6	25.2	31.2	40.5	31.1	28.5	26.8
	σ_n	1.8	2.1	1.7	3.7	4.8	3.1	2.6	3.7
<i>Trithemis annulata</i> (9 ♀♀, 2 ♀♀ ; Italy)									
		1	2	3	4	5	6	7	8
fw	\bar{x}	13.1	13.1	13.3	16.2	27.4	18.5	13.4	2.4
	σ_n	1.5	2	1.9	1.3	5.5	2.7	2.5	1.3
	\bar{x}	17.1	16.6	20.2	26	29	22.1	17.7	13.7
	σ_n	2.3	5.6	2.2	2.5	3.9	3.2	1.9	1.8
hw	\bar{x}	13.7	12.6	12.6	13.6	25.6	19.5	14.4	12.9
	σ_n	1.7	1.4	2.5	1.4	3.5	3.7	2.8	1.7
	\bar{x}	16.1	15.9	19.4	23.5	27.7	20	19	16.6
	σ_n	1.5	1.9	1.2	2.4	3.1	1.9	1.9	1.7
<i>Micrathyria aequalis</i> (5 ♀♀ ; Cuba)									
		1	2	3	4	5	6	7	8
fw	\bar{x}	12.2	14.4	15.4	15.4	23.6	22.8	15.2	3.4
	σ_n	1.6	0.8	1	2.1	3	1.2	2.7	1
	\bar{x}	20.4	20.2	22.4	24.4	25.4	26	18.6	19.4
	σ_n	0.5	1.7	1.9	3.6	2.1	2	1.6	
hw	\bar{x}	12.2	15.4	14.2	14.8	23.2	24.6	18.8	17
	σ_n	1.3	1.4	1.2	1.2	3.5	0.8	1.2	2.3
	\bar{x}	16.2	20	21.8	22.2	23.6	25.2	22.2	22
	σ_n	1.8	2.1	2.4	1.7	3.1	1.9	2.1	1.5

This phenomenon is quite common in the younger families (Corduliidae, Libellulidae and among the Coenagrionidea), but less so in the older families, particularly in Anisoptera. In the latter, spine density can increase on the upper row in the tract immediately adjacent to the hindwing base (tornus).

DISCUSSION

Our preceding studies revealed a fact which, despite its being foreseeable, is nonetheless of notable interest : along with characters common to all Odonata and presumably plesiomorphic, are other secondary ones linked to the two main Odonata subOrders and which respect the principle branching of Odonata phylogenesis. However, differences are visible even in lower systematic categories. Differences also occur between the fore and hindwings on the same side, indicating a probable different function of the fore and hindwings. The L and S spines are distributed generally on the inner wing veins (-) and (+), with the S spines assuming the shape of Sc or Se spines on the upper transverse vein, respectively, in Zygoptera and Anisozygoptera-Anisoptera. The relative density of the spines in the fore and hindwings distinguishes Calopterygoidea from Lestoidea and Coenagrionidea, and their density in some wing fields distinguishes the Sympetrinae-Trithemistinae complex from other Libellulidae subfamilies. Lastly, the density and morphology of the spines differs in the same wing fields of the fore and hindwing (D'ANDREA & CAFRI 1988, 1989, 1990).

Something similar occurs in the wing edge spines. The presence of Sc spines with an abside and posterior hind keel is diffuse and presumably primitive. As these are longitudinal veins it is not surprising : in fact spines of the same type, size and orientation are also present on the convex part of the longitudinal inner wing vein. The question arises as to whether this has a functional significance. If the spines of the leading edge function as turbulators by modifying the boundary layer so as to increase lift at low speeds, then the Sc spines on the inner wing 'crests' (i.e., the protruding part of the longitudinal veins) could have the same scope of increasing turbulence in the adjacent wing layers and in the vortices created by the crests in the valleys immediately behind them. These vortices were observed by NEWMAN *et al.* (1977), though in their model the internal crests had no spines.

The morphology of the hindwing edge spines is a valid key in differentiating a certain number of Anisoptera and Zygoptera families. The intermediate form, which apparently derives from the typical Sc spine and develops into the 'heart-shaped' one, appears in Lestoidea and Calopterygoidea (Zygoptera), in Anisozygoptera (midway between the extinct Isophlebiidae and Anisoptera) and in all Anisoptera : it appears as a very ancient character. Instead, the typical heart-shaped spines occur only in the median part of the trailing wing edge in some Anisoptera families. It is not certain if this character links these

families. The heart-shaped spines occur not only in Aeshnidae but in Petaluridae, Neopetaliidae, Gomphidae and Cordulegastridae, that is in groups probably not on the same evolutionary line with the former according to even most recently proposed phylogenetic systems (see e.g. PFAU, 1991, who links Petaluridae, Cordulegastridae and Gomphidae in a group called "Petaluroidea" as opposed to Aeshnidae). Thus, there are two possible interpretations regarding the heart-shaped spines: 1) they are a convergence in at least two families groups (according to an of the phylogenetic systems proposed); 2) they are a true synapomorphism and their absence in Libelluloidea is a secondary reduction.

NEWMAN *et al.* (1977) did not attribute particular aerodynamic functions to the hindwing edge spines but, according to our review of their morphology and distribution, this opinion is questionable. The differentiation of these spines suggests that they not only exercise a marked influence on the air flow exiting from the wing but that, above all, the influence differs between the fore and hindwing. Naturally, the certainty that the similarities and differences in spine distribution between the fore and hindwings on the same side are linked to an aerodynamic function can only be reached by experimental observation. However, this link is a strong working hypothesis in that the forewing drastically modifies the air flow reaching the hindwing. Thus, it seems logical to suppose that the wings present specializations in this regard, for example a certain number of modifications necessary to working in pairs. We have found such differences in the spines on both the inner and edge veins. The presence of elongated S spines on the lower row of the forewing cubito-anal field is not, above all, an isolated character. A dense covering of L spines occurs in the cubito-anal field on the lower side of the inner veins in Zygoptera and also in Libellulidae where they are longer and bent over so to form a spur-like shape pointing towards the trailing wing edge. Finally, Anisoptera have a certain number of rather marked Se spines on the lower side of the M_{spl} and CuP where, instead, Sc spines should be. It would appear that a strong selective pressure has been exerted on the lower cubito-anal field surfaces, above all in the forewings, through the thickening and/or elongation of both the L and S spines.

The spines, strangely overlooked in the past, are an important aspect of Odonata morphology for several reasons. Several aspects remain to be clarified, perhaps the most important of which is a thorough understanding of the functional differences between the fore and hindwing spines.

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