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SPINES ON THE WING VEINS IN ODONATA 2. ANISOZYGOPTERA AND ANISOPTERA *

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The spines on the convex and concave wing nervures in Anisozygoptera and Anisoptera differ morphologically and, according to their location, also in distribution and size. The latter is correlated to the surface and wing chords. The relative numbers of spines on the fore and hind wings and on both surfaces of the same wing are constant in the two suborders. Comparing these results with those on Zygoptera (M. D'ANDREA & S. CARFÌ, 1988, *Odonatologica* 17: 313-335) reveals a substantial uniformity of this trait in the entire order of Odonata.

INTRODUCTION

The presence of spines on the wing veins of Odonata was noted by SEGUY (1959) in *Cordulia aenea* and by HERTEL (1966) in *Aeshna cyanea*, where he says the nervures are "covered above and below with small spurs (about 0.015 mm in diameter and 0.15 mm long)" but adds that "we cannot yet say what the function of these spurs is". Finally, NEWMAN, SAVAGE & SCHOUELLA (1977) commented on the morphology and size of the spines in *Aeshna interrupta*, but did not go beyond suggesting that their function was to make the wing aerodynamic. Thus, to date, little more is known about the spines except that they exist.

This paper follows our recent report on the wing spines in Zygoptera (D'ANDREA & CARFÌ, 1988), completing a preliminary study of these structures in Odonata. Our research provides data on the phylogeny, morphology and distribution of the spines, and tends of affirm their aerodynamic importance.

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The morphology and size of the spines were studied under a SEM and their distribution under a stereomicroscope. The nomenclature of the wing venation follows that of TILLYARD & FRASER (1938-1940).

GENERAL APPEARANCE IN ANISOZYGOPTERA AND ANISOPTERA

The morphological distinction between the wing nervure spines in Zygoptera is quite simple: these are either short (8-18 μm, small, stubby and carinate teeths, termed S) or long (20-70 μm,longitudinal grooved processes termed L) (D'ANDREA & CARFÌ, 1988)[1]. The L spines occur on the upper surface of the (−) longitudinals and lower surface of the (+) longitudinals, while the S spines have the opposite distribution as shown in Figure 1.

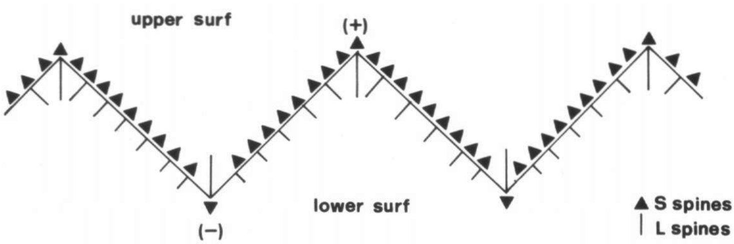

Fig. 1. Morphology and distribution of the spines in Zygoptera.

The same type of spines exist in Anisoptera. The S spines are usually less numerous and occasionally larger than those found in Zygoptera and occur on the upper surface of the (+) longitudinals and lower surface of the (−) longitudinals. The L spines occur on the opposite surfaces as well as on the lower side of the cross veins. The spines on the upper surface of the cross veins could be termed L spines if not for the following peculiarities: (a) they are smaller (1/2 to 1/3) than the underlaying ones, particularly near the wing borders, — (b) decrease in size in proximity to the anal field, particularly on the hind wing, until resembling small carinate spines which also occur on the hind borders, conferring (as in Zygoptera) a denticulate profile to the wing nervure, — (c) vary in size in relationship to the wing surface and chord like the carinate spines (Fig. 4), and they (d) resemble elongated spines in some primitive Zygoptera. Thus, these have been labelled S elongate (Se) spines. According to the distinction between Se and Sc spines, the S spines occurring in Zygoptera are Sc spines. They occur in single rows on the nervures, except on the upper surface of the R + M where there are two parallel rows of S carinate (Sc) spines.

The L spines shrink in size towards the margin, following the same gradient seen in Zygoptera, as do the Se spines on the upper surface of the cross veins. At the wing base the Sc spines on both surfaces of the longitudinals appear as distinct "teeth", shrinking towards the margins. In proximity to the hind margin they can become thinner and occasionally longer. The L spines on the upper (–) and lower (+) surfaces of the longitudinals are always longer than those on the adjacent cross veins. This fact, together with the variation in size occurring along the wing, makes it difficult to establish a norm for the size of the S and L spines which is indicative of the entire wing. Thus the dimensions given in Table IX are means calculated in the central zone of the fore wing at the level of the nodus.

The difference in size between the S and L spines tends to disappear in step with the reduction in morphological differences between the (+) and (–) longitudinals, typically at the margins (where the lower L spines are always slightly longer than the upper S spines) and in the transition zone at the convex base of the intercalaries on the upper surface (and vice versa on the lower surface) where the L spines shrink to the size of S spines (as in Zygoptera). Some longitudinal nervures occasionally show a slight incavation in which case the Sc spines appear longer and aciform (base of the R_3 on the lower surface, and now and then on other nervures).

There is an ample interindividual variability in the quantity of spines on the wing surface, as in Zygoptera, but the ratio between the fore and hind wings and between the two surfaces of the same wing is roughly the same in both conspecific and intraspecific specimens. This similarity in ratio allows a preliminary evaluation of the phenomenon without a statistical analysis of the many specimens of each species.

Tiny spines on the cross veins adjacent to the insertion point of the (+) and (–) longitudinals, similar to those observed in Zygoptera, are present up to but not beyond the distal half of the wing.

The specimen of *Epiophlebia superstes,* which does not differ substantially from the above, has Se spines on the cross veins of the upper wing surface. The Sc spines on the longitudinal nervures are small and dense; denticulated as in Zygoptera, and grow in size in proximity to the margin.

APPEARANCE IN ANISOZYGOPTERA AND ANISOPTERA FAMILIES

Anisozygoptera

EPIOPHLEBIIDAE

Epiophlebia superstes (Selys, 1889)

1 ♂, Japan

Upper surface. — A few tiny Sc spines are present on the R+M, R and R_1 (from Pt on). Distinct spines occur on R_2 and IR_3 and a transition zone along the base of IR_2. A_1 has large "teeth" (Sc) between the base and discoidal cell (DC) and is smooth thereafter. Tiny spines reappear about halfway along A_1. The first third of Ma is also smooth. Tiny L spines appear on Sc vein, Rs and R_{2+3}. R_2 is smooth almost up to the Pt. Several long L spines appear on R_2 (at about the level of the Pt), R_3, R_{4+5} and CuP. The cross veins have Se spines which are tiny at the hind margins and at the apex. The first 5-6 cross veins of the anal field are smooth while those between R and Rs have several tiny spines. Ans and Pns have evident spines between C and Sc and between R_1 and R_2.

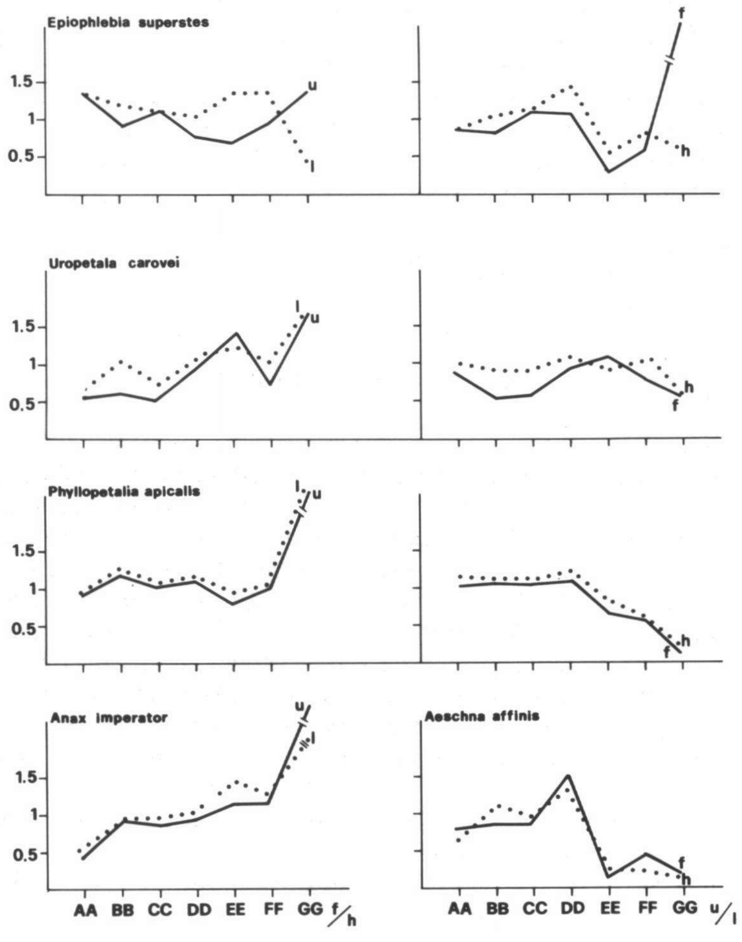

Fig. 2. Ratios between fore/hind (f/h) and upper/lower (u/l) in *Epiophlebia superstes* and some Aeshnoidea. — [u: upper wing surface; — l: lower wing surface; — f: fore wing; — h: hind wing].

Lower surface. — R_2 and R_3 have tiny Sc spines along the entire nervure, R_{4+5} is smooth up to the level of the nodus and then appears like the above. CuP has about a dozen spines after DC and is feebly denticulate on the margin. Sc vein is smooth. All the (+) longitudinals have L spines except R+M, R and the first fourth of R_1. The distribution and morphology of the L spines on the cross veins is like that of the overlying Se spines.

The spines in *E. superstes* are in greatest number and equally dense on the upper hind and lower fore wing surface (Tab. I). The fore/hind ratio is higher for the lower wing surface in all sectors except GG (Ans). The high value of AA (that is, more spines in the posterior anal field) and low value of GG on the lower surface (that is, many more spines on the hind Ans) does not occur in Anisoptera (Tab. III. Fig. 2). The upper/lower ratio (between the upper surface Se spines and lower surface L spines) reaches a maximum in DD (between R_1 and R_2) in the hind wing, and a minimum in EE (Pns and R_1 prior to the Pt). This trend — of a minimum AA, maximum DD, minimum EE and slight increase in values in FF — is common for both wings in Anisoptera (cf. Tabs V, VI, Figs 2, 3).

Anisoptera

PETALURIDAE

Uropetala carovei (White, 1843)

1 ♂, Australia

Upper surface. — Large Sc spines are present on R_1 (shrinking in size after the Pt), the initial tract of IR_3 and MA, the basal tract of A_1 (for A_1 and CuP, the tract leading up to the DC will hereafter be referred to as "basal" and that following the DC as "distal"). Smaller and occasionally thinner spines occur on R, the distal tracts of IR_3, MA and A_1. Several L spines are present on the (-) longitudinals, except on Sc and Rs which are smooth. A few spines appear on R_2 after the Pt, and many on the distal third of R_3, the distal two thirds of R_{4+5} and distal CuP. The cross veins have a few short Se spines in the marginal zones and at the apex. The nervures of the anal triangle are smooth while the spines on the adjacent ones (up to the level of the DC) thin out towards the wing base, as in the fore wing. A few tiny spines occur on the DC cross veins and between R and Rs, CuP and A_1 (basally). Ans and Pns have numerous spines, almost all between C and Sc vein and between R_1 and R_2.

Lower surface. — The (-) longitudinals have large Sc spines on the Sc vein, smaller ones on the Rs, R_2, and R_3, thinner ones on the R_{4+5}, and Se type spines on the Rspl, Mspl, and distal CuP. The spines on R_2 and R_3 are shorter and denser towards the apex. Several L spines are present on the IR_2, IR_3, MA (second half), A_1 (distally), R and R_1 while the remainder of these nervures is

Table I

Distribution of the L and Se spines in *Epiophlebia superstes* and in some Aeshnoidea — [A: field between CuP and the hind wing margin; B: between R_{4+5} and CuP; — C: between R_3 and R_4+$_5$; — D: between R_2 and R_3; — E: Pns and R_1 before the Pt; — F: Pns and R_1 after the Pt; — G: Ans and Sc; — a: cross veins between R and Rs; — T: totals; — Surf: wing surface (mm²); — d: density of the spines on the wing; — fu: forewing upper surface; — fl: forewing lower surface; — hu: hindwing upper surface; — hl: hindwing lower surface] — The values refer to the right wing of each specimen. Sex is specified only for the females.

Species		A	B	C	D	E	F	G	a	T	Surf	d
Epiophlebia	fu	548	862	932	601	52	78	52	5	3130	165.15	18.95
superstes	fl	609	1054	846	564	181	133	12	65	3464		20.97
	hu	408	916	854	785	76	83	38	9	3169	166.98	18.98
	hl	455	876	735	548	137	100	55	57	2963		17.74
Uropetala	fu	455	867	955	1156	130	91	65	2	3721	590.2	6.3
carovei	fl	539	1649	1592	1223	120	119	102	3	5330		9.03
	hu	837	1443	1731	1175	88	121	38	-	5433	714.8	7.6
	hl	853	1584	1954	1135	98	119	59	7	5809		8.13
Phyllopetalia	fu	533	857	1021	673	70	69	3	28	3254	380.2	8.56
apicalis	fl	511	800	950	614	101	104	29	27	3136		8.25
	hu	579	734	999	631	91	70	-	21	3125	439.2	7.12
	hl	522	653	898	534	107	102	9	20	2845		6.48
Aeshna	fu	171	532	782	281	6	9	8	2	1788	343	5.21
affinis	fl	208	612	877	185	41	21	49	-	1993		5.81
	hu	253	738	1005	280	7	6	3	-	2292	440.9	5.2
	hl	393	684	1049	202	41	31	17	-	2417		5.48
A.	fu	250	421	732	185	7	3	4	-	1602	275.4	5.82
bonariensis	fl	180	467	947	185	49	27	19	-	1847		6.8
	hu	383	460	776	175	3	5	3	-	1805	325.3	5.55
	hl	239	509	971	180	34	11	3	-	1947		5.99
A.	fu	327	773	1175	533	85	50	106	11	3060	376.8	8.12
cyanea	fl	496	942	1290	576	130	89	108	31	3662		9.72
	hu	540	796	1350	613	81	32	29	6	3447	501	6.88
	hl	644	913	1595	502	140	85	43	15	3937		7.86
A.	fu	154	498	722	213	12	7	3	2	1611	343.6	4.69
mixta	fl	260	565	933	203	51	14	19	4	2049		5.96
	hu	378	547	769	211	10	4	1	1	1921	459	4.19
	hl	422	624	885	214	57	8	3	2	2213		4.82
Anax	fu	285	621	1078	275	18	11	34	5	2327	390.8	5.95
imperator	fl	338	790	1405	161	71	43	69	3	2880		7.37
	hu	734	677	1227	288	15	9	7	3	2969	468.4	6.34
	hl	700	862	1513	161	58	34	29	3	3360		7.17

(Continued Table I).

Species		A	B	C	D	E	F	G	a	T	Surf	d
Hemianax	fu	324	511	687	125	5	1	10	5	1668	307.1	5.43
ephippiger	fl	262	517	808	96	31	12	35	6	1767		5.75
	hu	871	626	869	126	4	-	3	-	2499	409.2	6.11
	hl	604	636	1017	96	33	5	7	2	2400		5.87
Brachytron	fu	224	525	961	358	50	18	26	12	2174	212.3	10.24
pratense	fl	259	593	1047	243	73	27	13	6	2261		10.65
	hu	305	579	979	379	52	13	11	9	2327	251.3	9.26
	hl	409	597	1040	268	71	22	9	4	2420		9.63
Boyeria	fu	338	502	691	380	33	3	43	1	1991	361.3	5.51
irene	fl	417	618	951	372	98	15	41	6	2518		6.97
	hu	392	659	808	432	30	3	18	1	2343	449.8	5.21
	hl	654	686	932	383	96	16	22	2	2791		6.2
Progomphus	fu	160	407	415	284	9	2	6	-	1283	314.1	4.09
zonatus	fl	199	454	413	231	34	10	9	-	1350		4.3
	hu	305	432	430	293	12	5	-	-	1477	331.9	4.45
	hl	283	550	410	227	41	9	3	-	1523		4.59
Gomphoides	fu	269	600	598	467	15	8	2	2	1961	337.5	5.81
sp.	fl	256	681	629	357	64	20	23	-	2030		6.01
	hu	401	725	616	451	9	7	2	-	2211	407.4	5.43
	hl	361	629	666	363	63	13	15	1	2111		5.18
Onychogomphus	fu	110	196	268	211	9	4	3	-	803	180.9	4.44
forcipatus	fl	166	325	389	365	47	30	8	-	1248		6.9
	hu	174	241	328	274	7	7	1	-	1004	219.1	4.58
	hl	182	325	416	287	33	25	3	-	1284		5.86
O.	fu	292	395	475	307	5	2	5	-	1457	167.4	8.7
forcipatus ♀	fl	308	476	544	306	32	19	3	13	1701		10.16
	hu	439	398	530	309	4	8	-	-	1697	211.4	8.03
	hl	405	482	640	302	29	17	2	-	1877		8.88

smooth. The L spines on the cross veins have the same size and distribution as the overlying Se spines.

Spines are most numerous on both surfaces of the hind wing, but their density is highest on the lower surface of the fore wing (Tab. I), as is common in Anisoptera. The fore/hind ratio (Tab. III, Fig. 2) gives higher values for the lower than for the upper surface. Nonetheless, the trend — minimum values for AA, maximum for EE, minimum for FF and maximum for GG — resembles that present in all Anisoptera and definitely differs from that seen in *Epiophlebia superstes*. However, the upper/lower graph shows an evident anomaly — the maximum for EE — in the fore wing (Tab. V, Fig. 2).

Table II
Distribution of the L and Se spines in *Cordulegaster boltonii* and some Libelluloidea. — [See Table I for an explanation of the symbols]

Species		A	B	C	D	E	F	G	a	T	Surf	d
Cordulegaster	fu	492	888	1015	575	115	68	115	-	3268	415.3	7.87
boltonii	fl	584	856	1145	500	131	68	171	21	3476		8.37
	hu	687	945	1155	668	115	80	49	2	3701	496.9	7.45
	hl	708	836	1170	524	123	105	73	21	3560		7.16
C.	fu	811	1078	1696	778	85	32	76	-	4574	509	8.99
boltonii ♀	fl	984	1089	1728	689	132	83	163	24	4892		9.61
	hu	1097	1247	1694	890	116	51	18	7	5120	615.6	8.32
	hl	1280	1251	1820	636	141	79	69	16	5292		8.6
Cordulia	fu	282	432	716	567	11	10	6	-	2024	246.4	8.22
aenea	fl	359	529	842	541	74	35	17	7	2404		9.76
	hu	486	641	772	596	14	12	2	-	2418	333.2	7.26
	hl	429	686	973	615	83	39	10	3	2838		8.52
C.	fu	348	465	686	489	11	15	14	-	2028	238.4	8.51
aenea ♀	fl	325	446	947	482	72	36	16	7	2331		9.78
	hu	742	621	794	578	12	16	10	-	2811	318.7	8.82
	hl	481	596	955	507	66	41	7	8	2661		8.35
Hemicordulia	fu	344	419	509	301	20	9	21	-	1549	382.5	4.05
mindana	fl	398	463	637	228	39	17	10	-	1792		4.69
	hu	396	421	570	236	8	9	2	-	1642	512.2	3.2
	hl	372	337	619	244	39	14	-	-	1625		3.17
Somatochlora	fu	215	274	430	356	7	14	1	-	1297	241.9	5.36
metallica	fl	244	303	549	295	45	33	2	3	1474		6.09
	hu	228	331	463	319	7	14	-	-	1362	306	4.45
	hl	250	334	595	320	48	26	1	-	1574		5.14
Oxygastra	fu	184	274	427	275	7	14	1	1	1193	208.4	5.73
curtisii	fl	225	306	485	251	63	38	8	-	1376		6.6
	hu	336	273	482	298	8	8	1	-	1406	291	4.83
	hl	250	317	545	290	56	32	-	-	1490		5.12
Micromacromia	fu	86	221	162	228	6	7	-	-	710	164.9	4.31
camerunica	fl	89	216	290	229	60	27	2	-	913		5.54
	hu	125	250	239	233	2	2	-	-	851	192.7	4.42
	hl	189	262	354	274	40	23	3	2	1147		5.95
Uracis	fu	129	353	392	481	14	10	-	-	1379	192.9	7.15
ovipositrix	fl	222	359	441	409	62	15	8	2	1518		7.87
	hu	342	332	448	461	14	12	-	-	1609	263.5	6.11
	hl	393	316	474	388	41	19	6	3	1640		6.22

(Continued Table II).

Species		A	B	C	D	E	F	G	a	T	Surf	d
Brachymesia	fu	129	207	297	239	-	2	-	-	874	210.4	4.14
furcata	fl	164	350	408	318	53	7	4	1	1305		6.2
	hu	186	356	210	270	2	-	-	-	1024	260.1	3.94
	hl	385	378	465	288	47	7	3	-	1573		6.05
B.	fu	183	442	526	431	-	1	-	-	1583	257.7	6.14
herbida	fl	300	412	602	374	49	2	3	-	2327		9.03
	hu	240	344	544	423	-	-	-	-	1551	345.7	4.49
	hl	348	346	603	330	29	1	-	-	1657		4.79
Ladona	fu	139	500	530	492	11	5	-	16	1693	215.5	7.86
fulva	fl	289	620	638	447	42	24	12	19	2091		9.7
	hu	358	534	589	507	7	4	-	5	2004	286.2	7
	hl	544	674	728	501	46	23	7	15	2538		8.87
Orthetrum	fu	209	334	454	352	1	6	-	-	1356	256.6	5.28
cancellatum	fl	250	527	653	452	50	25	4	-	1961		7.64
	hu	324	336	497	436	-	3	-	-	1596	320.5	4.98
	hl	400	516	712	506	32	20	-	-	2186		6.82
O.	fu	145	311	396	369	1	2	-	1	1225	173.7	7.05
coerulescens	fl	188	459	497	300	44	6	5	4	1503		8.65
	hu	160	304	472	352	2	-	-	1	1291	236.1	5.47
	hl	321	467	566	335	29	5	2.	1	1726		7.31
Crocothemis	fu	123	401	436	455	6	5	-	-	1426	192.5	7.41
erythraea	fl	295	611	571	462	47	15	7	-	2008		10.43
	hu	312	496	477	462	4	5	-	-	1756	244.6	7.18
	hl	680	646	770	505	51	15	2	-	2669		10.91
C.	fu	146	374	394	307	6	3	5	-	1235	205.7	6
erythraea ♀	fl	319	524	541	371	68	13	18	11	1865		9.07
	hu	282	449	487	354	8	5	-	-	1585	234.9	6.75
	hl	584	555	598	264	43	12	7	-	2062		8.78
Diplacodes	fu	116	199	248	229	1	-	-	-	793	95.8	8.28
lefebvrei	fl	111	270	288	228	22	4	-	-	923		9.63
	hu	117	183	284	230	-	1	-	-	815	113.6	7.17
	hl	228	265	361	237	7	5	-	-	1103		9.71
Sympetrum	fu	179	273	279	197	-	-	-	-	928	160	5.8
sanguineum	fl	285	369	407	187	36	10	-	2	1296		8.1
	hu	192	278	359	208	-	1	-	-	1038	206.4	5.03
	hl	556	415	493	206	27	9	0	2	1708		8.28

(Continued Table II).

Species		A	B	C	D	E	F	G	a	T	Surf	d
S.	fu	136	269	294	228	-	1	-	-	928	153	6.07
sanguineum ♀	fl	282	349	381	377	46	14	3	3	1325		8.66
	hu	217	316	358	289	-	-	-	-	1180	255.6	4.62
	hl	595	424	453	276	31	10	-	-	1789		7
S.	fu	116	242	341	307	-	-	-	-	1006	213.3	4.72
striolatum	fl	347	376	493	327	29	17	-	-	1599		7.5
	hu	184	248	372	377	-	-	-	-	1181	259.7	4.55
	hl	497	396	531	345	23	12	-	-	1814		6.98
Trithemis	fu	181	271	452	249	1	-	-	-	1155	183.7	6.29
annulata	fl	316	389	478	188	35	6	-	1	1624		8.84
	hu	215	340	491	319	1	-	-	-	1366	252	5.42
	hl	1046	412	521	215	24	5	-	-	2223		8.82
T.	fu	219	176	337	218	-	-	-	-	950	177.5	5.35
annulata ♀	fl	278	383	415	156	34	1	-	1	1268		7.14
	hu	179	281	370	246	-	-	-	-	1076	244.5	4.4
	hl	965	430	431	174	21	1	-	-	2022		8.27
Perithemis	fu	109	264	364	351	5	2	-	-	1095	93.6	11.7
mooma	fl	160	254	366	210	50	6	-	-	1046		11.18
	hu	182	316	452	324	1	4	-	-	1279	105.4	12.13
	hl	317	303	387	237	52	13	-	-	1309		12.42
Miathyria	fu	115	159	191	208	-	-	-	-	673	229.2	2.94
marcella	fl	195	183	181	175	24	4	-	-	762		3.32
	hu	60	170	195	184	-	1	-	-	611	321.2	1.9
	hl	109	190	202	142	3	2	-	-	647		2.01
Pantala	fu	277	311	358	429	-	-	-	-	1375	302.9	4.54
flavescens	fl	327	345	460	390	25	6	8	-	1561		5.15
	hu	284	241	454	416	-	-	-	-	1395	445.6	3.13
	hl	537	384	483	365	3	2	-	-	1774		3.98
Tramea	fu	256	436	439	589	11	-	-	-	1731	335.1	5.17
cophysa	fl	238	390	449	479	39	7	3	-	1605		4.79
	hu	265	532	623	674	4	-	-	-	2098	438.6	4.78
	hl	356	482	508	516	23	5	-	-	1890		4.31
Tholymis	fu	184	263	414	393	4	9	-	-	1267	295.2	4.29
tillarga	fl	282	335	467	350	23	8	-	-	1465		4.96
	hu	244	317	568	437	6	3	-	-	1575	421.6	3.74
	hl	373	271	621	412	9	4	-	-	1690		4.01

(Continued Table II).

Species		A	B	C	D	E	F	G	a	T	Surf	d
Macrodiplax	fu	53	226	190	195	-	-	-	-	664	227.6	2.92
cora	fl	174	285	277	141	4	4	-	-	885		3.89
	hu	70	175	216	191	-	-	-	-	652	269.1	2.42
	hl	261	228	284	131	3	2	-	-	909		3.38
Selysiothemis	fu	28	116	122	164	-	-	-	-	430	167.3	2.57
nigra	fl	146	179	151	90	4	2	-	-	572		3.42
	hu	51	94	159	140	-	-	-	-	452	216.3	2.09
	hl	69	112	144	79	2	1	-	-	407		1.88

NEOPETALIIDAE

Phyllopetalia apicalis Selys, 1857

1 ♂, Chile

Upper surface. — Several large Sc spines occur on R, R_1 and IR_2 (up to the Pt, after which the nervures become denticulate and then smooth), IR_3 (for the first third), and A_1 (basally). On the remainder of IR_3, MA and A_1 are smaller spines. There is a long transition zone at the base of IR_2. The (–) longitudinal nervures have L spines on the second half of R_2, R_3 and R_{4+5} and on all (except in the basal tract) of CuP, while Sc vein and Rs are smooth. The cross veins have shorter Se spines in the marginal and apical zones of the wing. In proximity to the anal field the spines are very tiny (particularly near the anal triangle) and some nervures are denticulated. There are a few spines on Ans — between C and Sc veins, more on Pns — almost all between R_1 and R_2 — which flatten out towards the apex. Minute spines are present on the cross veins of the DC, between CuP and A_1 (basally) and, in slightly greater number, on R and Rs.

Lower surface. — The (–) longitudinals have large Sc spines on Sc and the basal tract of CuP, while R_{2+3}, R_2, R_2, R_3, R_{4+5} are denticulated with a few thinner spines on the margin. The Rspl, Mspl and CuP have Se spines. A few L spines are present on the R_1, in slightly greater number under the Pt and flattening out towards the apex. A much greater number of L spines occur on IR_2, IR_3, MA (after the first third) and A_1 (distally), while R is smooth. The L spines on the cross veins are alike in size and distribution to the overlying Se spines.

The quantity and density of the spines is greater on both surfaces of the fore wing (Tab. I). The values of the fore/hind ratio (Tab. III, Fig. 2) are always higher — usually greater than 1 — for the lower surface. As in the rest of the suborder, there is a minimum of AA and maximum of GG, and high values for AA, a maximum in DD and decrease in EE in the upper/lower ratio (Tab. V, Fig. 2).

Table III
Ratios of distribution of the L and Se spines on the fore and hind wing in *Epiophlebia superstes* and some Aeshnoidea. — [AA, BB, CC, DD, EE, FF, GG, and TT are the ratios between the fields of A, B, C, D, E, F, G, and T; u: upper surface; l: lower surface]

Species		AA	BB	CC	DD	EE	FF	GG	TT
Epiophlebia	u	1.34	0.94	1.09	0.77	0.68	0.94	1.37	0.99
superstes	l	1.34	1.2	1.15	1.03	1.32	1.33	0.22	1.17
Uropetala	u	0.54	0.6	0.55	0.98	1.48	0.75	1.71	0.68
carovei	l	0.63	1.03	0.81	1.08	1.22	1	1.73	0.92
Phyllopetalia	u	0.92	1.17	1.02	1.07	0.77	0.99	3	1.04
apicalis	l	0.98	1.23	1.06	1.15	0.94	1.02	3.22	1.1
Aeshna	u	0.68	0.72	0.78	1	0.86	1.5	2.67	0.78
affinis	l	0.53	0.89	0.84	0.92	1	0.68	2.9	0.82
A.	u	0.65	0.92	0.94	1.06	2.33	0.6	1.33	0.89
bonariensis	l	0.75	0.92	0.98	1.03	1.44	2.45	6.33	0.96
A.	u	0.81	0.97	0.87	0.87	1.05	1.56	3.66	0.89
cyanea	l	0.77	1.03	0.81	1.15	0.93	1.05	2.51	0.93
A.	u	0.41	0.91	0.94	1.01	1.2	1.75	3	0.84
mixta	l	0.62	0.91	1.05	0.95	0.89	1.75	6.33	0.93
Anax	u	0.39	0.92	0.88	0.95	1.2	1.22	4.86	0.79
imperator	l	0.48	0.92	0.93	1	1.43	1.26	2.38	0.86
Hemianax	u	0.37	0.82	0.79	1	1.25	1	3.33	0.67
ephippiger	l	0.43	0.81	0.79	1	0.94	2.4	5	0.74
Brachytron	u	0.73	0.91	0.98	0.94	0.96	1.38	2.36	0.93
pratense	l	0.63	0.99	1.01	0.91	1.03	1.23	1.44	0.92
Boyeria	u	0.86	0.76	0.86	0.88	1.1	1	2.39	0.85
irene	l	0.64	0.9	1.02	0.97	1.02	0.94	1.86	0.9
Progomphus	u	0.52	0.94	0.97	0.97	0.75	0.4	6	0.85
zonatus	l	0.7	0.83	1.01	1.02	0.83	1.11	3	0.89
Gomphoides	u	0.67	0.83	0.97	1.04	1.67	1.14	1	0.89
sp.	l	0.71	1.08	0.94	1	1	1.54	1.53	0.96
Onychogomphus	u	0.63	0.81	0.82	0.86	1.29	0.57	3	0.8
forcipatus	l	0.91	1	0.94	0.94	1.42	1.2	2.67	0.97
O.	u	0.67	0.99	0.9	0.99	1.25	0.25	5	0.86
forcipatus ♀	l	0.76	0.99	0.85	1.01	1.11	1.12	1.5	0.91

AESHNIDAE

Aeshna cyanea (Müller, 1764)

1 ♂, 1 ♀, Italy

Upper surface. — Large Sc spines are present on R, R_1, and A_1 (basally). Thinner spines cover IR_2, IR_3 and MA (on top of a tiny saw-toothed zone) and A_1 (distally). In the initial tract of the Rspl and Mspl branches are brief transition zones. Numerous L spines are present on R_2, R_3, Rspl and Mspl and distally on CuP, Sc vein and Rs are smooth and R_{4+5} have a few spines on the margin of the fore wing but are smooth in the posterior. The cross veins have Se spines which apically are very short and like carinate teeth. The spines are very small along the entire wing margin, becoming smaller and farther apart basally. The anal triangle and adjacent cells have smooth nervures. The Ans and Pns have numerous tiny spines, mostly between C and Sc veins and between R_1 and R_2. Just beyond the Pt these spines shrink and disappear. Tiny spines occur on cross veins of the DC, between CuP and A_1 (basally) and between R and Rs.

Lower surface. — Large Sc spines are present on Sc vein, Rs and CuP (basally). Smaller spines appear on R_2 and slightly thinner ones in somewhat greater density on R_3 and R_{4+5}. There are Se spines on Rspl, Mspl and distally on CuP. A few L spines are present on R_1, almost all beyond the Pt and gradually decreasing in size, and several on all (or at least the distal two thirds) of IR_2, IR_3, MA and A_1 (distally) while R is smooth. The L spines on the cross veins are alike in size and number to the overlying Se spines.

Other species studied: *Boyeria irene* (Fonscolombe, 1838) (1 ♂, Italy), *Brachytron pratense* (Müller, 1764) (1 ♂, Italy) (Brachytroninae); *Aeshna affinis* Vander Linden, 1823 (1 ♂, 1 ♀, Italy), *A. bonariensis* Rambur, 1842 (1 ♂, Brazil), *A. juncea* (L., 1758) (1 ♂, 1 ♀, Italy), *A. mixta* Latreille, 1805 (1 ♂, 1 ♀), *Castoraeschna castor* (Brauer, 1865) (1 ♂, Brazil) *Coryphaeschna secreta* Calvert, 1952 (1 ♂, Cuba), *C. viriditas* Calvert, 1952 (1 ♂, Cuba), *Anax guttatus* (Burmeister, 1839) (2 ♂, Philippines), *A. imperator* Leach, 1815 (1 ♂, 1 ♀, Italy), *A. parthenope* Selys, 1839 (1 ♂, Italy), *A. strenuus* Hagen, 1867 (1 ♂, Hawaii), *Anaciaeschna isosceles* (Müller, 1767) (1 ♂, 1 ♀, Italy), *Hemianax ephippiger* (Burmeister, 1839) (1 ♀, Congo), *Gynacantha* sp. (1 ♀, Congo), *G. cylindrata* Karsch, 1891 (1 ♂, Congo), *G. manderica* Gruenber, 1902 (1 ♂, 1 ♀, Somalia), *Staurophlebia reticulata* (Burmeister, 1839) (1 ♀, Brazil) (Aeshninae).

There are no relevant differences in the distribution of the spines on the upper wing surface of Aeshnini. They thin out in proximity to the anal field and shrink in size marginally, but the only smooth nervures are in the anal triangle. The spines grow gradually towards the DC, and in *Coryphaeschna* spp. the branches proximal to A_1 on the hind wing have dense evident saw-teeth. In *Coryphaeschna* spp. and *Aeshna juncea* (Aeshnini) the spines in the upper posterior anal field are longer and more numerous immediately after the basal marginal zone. This trait is even more noticeable in Anactini (in *Anax* spp. the density and size of these spines decreases and then increases towards the DC), where the spines of the lower branches of A_1 are elongated and always associated with S spines resembling long spurs in the basal tract of A_1 on the upper surface. In *Boyeria irene*, where the spines proximal to the anal field are long and dense, the A_1 has rather large Sc spines which, however, are not spurred. Spurs are not present in the other species of Aeshnini, *Anaciaeschna isosceles* or in Gynacanthagini, where the spines in the anal field gradually grow in size towards the wing base in the direction of the DC. In all the species the wing apex shows a more or less noticeable reduction in the size and number of spines. The upper surface of R_{4+5} is smooth (or at most has 2-3 marginal spines) in the hind wing of *Aeshna* spp., *Anax parthenope, Anaciaeschna isosceles* and both the wings of Gynacanthagini while all the other species have very few (8-10) spines. There is a greater number on both the wings of *Brachytron pratense*. On the lower surface, the R_1 is smooth before the Pt in the hind wing of all the species observed except *Aeshna juncea* and the Brachytroninae. All the species have Se spines on the Rspl, Mspl and CuP which are longest and most numerous on the latter two nervures (with some exception for CuP which can be smooth immediately distally to the DC).

The spines are most numerous on both surfaces of the hind wing, and densest on the fore wings (Tab. I). As was true for the preceding families, the fore/hind values are always higher for the upper surface (except in *B. pratense*) — minimum value in AA, maximum in GG and EE (particularly on the lower surface) — and the upper/lower ratio — maximum in DD, minimum in EE — within the norms of the suborder. The value of DD is generally higher than in the preceding families (Tab. V, Fig. 2).

GOMPHIDAE

Progomphus zonatus Hagen *in* Selys, 1854

2 ♂, Guyana

Upper surface. — Large Sc spines are present on R, R_1 (up to the Pt and thereafter smooth) and A_1 (basally). Smaller spines occur on IR_2 and A_1 (distally). The IR_3 ad MA are smooth except for an occasional minute denticulation distally, as are Sc vein, Rs, R_{2+3} and R_2, while a few L spines appear at the beginning of R_3, on R_{4+5} before the margin and distally on the CuP. The crossveins have Se spines which are smaller in the marginal and apical zones of the wing and in proximity to the anal field. The cross veins between R and Rs are smooth while a few small spines occur on the DC. The Ans on the fore wing have a few tiny teeth between C and Sc veins, but are smooth on the hind wing. A greater number of spines occur on the Pns, almost all before the Pt and between R_1 and R_2. There are transition zones at the base of IR_2 and on the lower branches of IR_3.

Lower surface. — Large Sc spines appear on the Rs and basally on CuP in the hind wing, while smaller spines appear on the fore wing. The R_{4+5} of both wings

Table IV
Ratios of distribution of the L and Se spines on the fore and hind wing in *Cordulegaster boltonii* and in some Libelluloidea. — [See Table III for an explanation of the symbols]

Species		AA	BB	CC	DD	EE	FF	GG	TT
Cordulegaster	u	0.72	0.94	0.88	0.86	1	0.85	2.35	0.88
boltonii	l	0.82	1.02	0.98	0.95	1.07	0.65	2.34	0.98
C.	u	0.74	0.86	1	0.89	0.73	0.63	4.2	0.89
boltonii ♀	l	0.77	0.87	0.95	1.08	0.94	1.05	2.36	0.92
Cordulia	u	0.6	0.81	0.93	0.95	0.79	0.83	3	0.86
aenea	l	0.84	0.77	0.87	0.88	0.89	0.9	1.7	0.85
C.	u	0.47	0.75	0.86	0.85	0.92	0.94	1.4	0.72
aenea ♀	l	0.68	0.75	0.99	0.95	1.09	0.88	2.29	0.88
Hemicordulia	u	0.87	0.99	0.89	0.96	2.5	1	10.5	0.94
mindana	l	1.07	1.37	1.03	0.93	1	1.21	10	1.01
Somatochlora	u	0.99	0.83	0.93	1.12	1	1	1	0.95
metallica	l	0.98	0.91	0.92	0.92	0.94	1.27	2	0.94
Oxygastra	u	0.55	1	0.89	0.92	0.88	1.75	11	0.85
curtisii	l	0.9	0.97	0.89	0.87	1.13	1.19	8	0.92
Micromacromia	u	0.69	0.88	0.68	0.98	3	3.5	-	0.83
camerunica	l	0.47	0.82	0.82	0.84	1.5	1.17	0.67	0.8
Uracis	u	0.38	1.06	0.88	1.04	1	0.83	-	0.86
ovipositrix	l	0.56	1.14	0.93	1.05	1.51	0.79	1.33	0.93
Brachymesia	u	0.76	1.28	0.97	1.02	-	1	-	1.02
herbida	l	0.86	1.19	1	1.13	1.69	2	3	1.4
B.	u	0.69	0.58	1.41	0.86	0.5	2	-	0.85
furcata	l	0.43	0.93	0.88	1.1	1.13	1	1.33	0.83
Ladona	u	0.39	0.94	0.9	0.97	1.57	1.25	-	0.84
fulva	l	0.53	0.92	0.88	0.89	0.91	1.04	1.71	0.82
Orthetrum	u	0.65	0.99	0.91	1.01	1	2	-	0.85
cancellatum	l	0.63	1.02	0.92	0.89	1.56	1.25	4	0.9
O.	u	0.91	1.02	0.84	1.05	0.5	2	-	0.95
coerulescens	l	0.59	0.98	0.88	0.9	1.52	1.2	2.5	0.87
Crocothemis	u	0.39	0.81	0.91	0.98	1.5	1	-	0.81
erythraea	l	0.43	0.95	0.74	0.91	0.92	1	3.5	0.75

(Continued Table IV).

Species		AA	BB	CC	DD	EE	FF	GG	TT
C.	u	0.52	0.83	0.81	0.87	0.75	0.6	5	0.78
erythraea ♀	l	0.55	0.94	0.9	1.41	1.58	1.08	2.57	0.9
Diplacodes	u	0.99	1.09	0.87	1	1	1	-	0.97
lefebvrei	l	0.49	1.02	0.8	0.96	3.14	0.8	-	0.84
Sympetrum	u	0.93	0.98	0.78	0.95	-	-	-	0.89
sanguineum	l	0.51	0.89	0.83	0.91	1.33	1.11	-	0.76
S.	u	0.63	0.85	0.82	0.79	-	-	-	0.79
sanguineum ♀	l	0.47	0.82	0.84	0.89	1.48	1.4	3	0.74
S.	u	0.63	0.98	0.92	0.81	-	-	-	0.85
striolatum	l	0.7	0.95	0.93	0.95	1.26	1.42	-	0.88
Trithemis	u	0.84	0.8	0.92	0.78	1	-	-	0.85
annulata	l	0.3	0.94	0.92	0.87	1.46	1.2	-	0.64
T.	u	0.92	0.63	0.91	0.89	-	-	-	0.83
annulata ♀	l	0.29	0.89	0.96	0.9	1.62	1	-	0.63
Perithemis	u	0.6	0.84	0.81	1.08	5	0.5	-	0.86
mooma	l	0.5	0.84	0.95	0.89	0.96	0.46	-	0.8
Miathyria	u	1.92	0.94	0.98	1.13	1	-	1	1.1
marcella	l	1.81	0.96	0.9	1.23	8	4	-	1.18
Pantala	u	0.98	1.29	0.79	1.03	-	-	-	0.99
flavescens	l	0.61	0.9	0.95	1.07	8.33	3	8	0.88
Tramea	u	0.97	0.82	0.7	0.87	2.75	-	-	0.83
cophysa	l	0.67	0.81	0.88	0.93	1.7	1.4	-	0.85
Thohymis	u	0.76	0.83	0.73	0.9	0.67	3	-	0.8
tillarga	l	0.76	1.24	0.75	0.85	2.56	2	-	0.87
Macrodiplax	u	0.76	1.29	0.88	1.02	-	-	-	1.02
cora	l	0.67	1.25	0.98	1.08	1.33	2	-	0.98
Selysiothemis	u	0.55	1.23	0.77	1.12	-	-	-	0.95
nigra	l	2.12	1.6	1.05	1.14	2	2	-	1.41

is densely denticulate. Distally the CuP of the fore wing has shorter than usual Sc spines while they are of normal length on the hind wing. Sc, R_2 and R_3 veins are smooth as are R, R_1 and the basal tract of A_1. There are some L spines in the first half of IR_2 and marginally on IR_3 and MA, and several on the distal branches of A_1. The L spines on the cross veins are alike in size and number to the overlying Se spines.

Other species studied: *Gomphus vulgatissimus* (L., 1758) (1 ♀, Italy), *Phyllogomphus selysi* Schouteden, 1933 (1 ♀, Congo) (Gomphinae); *Onychogomphus forcipatus unguiculatus* (Vander Linden, 1823) (1 ♂, 1 ♀, Italy), *O. uncatus* (Charpentier, 1840) (1 ♀, Marocco), *O. modestus* (Selys, 1878) (1 ♂, India) (Onychogomphinae); *Ictinogomphus ferox* (Rambur, 1842) (1 ♂, Somalia), *I. rapax* (Rambur, 1842) (1 ♂, Malaysia), *Gomphidia quarrei* (Schouteden, 1934) (1 ♂, Congo) (Lindeniinae); *Gomphoides* sp. (1 ♂, Brazil) (Gomphoidinae).

In contrast to the other species, *Onychogomphus* spp. have large Sc spines in tracts of the IR_3 and MA on the upper wing. Below, smaller Sc spines appear on the IR_2, R_3 and R_{4+5}. In *G. vulgatissimus* and *P. selysi* the R_{4+5} and part of IR_3 are entirely covered with small S spines. In all the species the S spines at the base of A_1 on the upper wing are very large and, as in some Aeshnidae, grow into large spurs in *Gomphoides* sp., and *G. vulgatissimus*. Sc and Rs veins are always smooth. In contrast to the other Aeshnoidea, with the possible exception of Gynacanthagini the L spines are very reduced in the other nervures. The R_2 is almost always smooth, as is the R_{4+5} in Onychogomphinae which in all the other species have at most a few spines. Below, the Rs and R_1 are always smooth (or with 1-2 spines on R_1), while only Gomphoidini and Onychogomphini have tiny spines from the Pt to the apex. In contrast to *P. zonatus*, all the other species have Se spines on the lower surface of CuP on both wings. The quantity values for both surfaces show more spines on the hind wing and coincide with the density values (Tab. I). The fore/hind ratio (Tab. III, Fig. 2) shows a trend similar to the other families — a minimum in AA and FF and maximum in GG — and the upper/lower ratio lies within the usual range — high values in AA, maximum in DD, minimum in EE, more or less stationary values in F-G (Tab. V, Fig. 2).

CORDULEGASTRIDAE

Cordulegaster boltonii (Donovan, 1807)

2 ♂, 1 ♀, Italy

Upper surface. — Large Sc spines are present on R, MA (initial tract) and A_1 (basally). Smaller spines appear on R_1, IR_2, IR_3, MA (distal two thirds) and A_1 (distally) which rise up from the serrated surface of the nervure. A few L spines occur on R_2 and R_3 (beginning at the level of the Pt and beyond), R_{4+5} (to the margin) and CuP (distally). The cross veins have Se spines, shorter at the margins and particularly at the apex, which thin out somewhat in proximity to the anal

Table V
Ratios of distribution of the L and Se spines between the upper and lower surface of the same wing in *Epiophlebia superstes* and some Aeshnoidea. — [f: fore wing; — h: hind wing. — See Table III for an explanation of the symbols]

Species		AA	BB	CC	DD	EE	FF	GG	TT
Epiophlebia	f	0.9	0.82	1.1	1.07	0.29	0.59	4.33	0.9
superstes	h	0.9	1.05	1.16	1.43	0.55	0.83	0.69	1.07
Uropetala	f	0.84	0.53	0.57	0.95	1.08	0.76	0.64	0.7
carovei	h	0.98	0.91	0.89	1.04	0.9	1.02	0.64	0.91
Phyllopetalia	f	1.04	1.07	1.07	1.1	0.69	0.66	0.1	1.04
apicalis	h	1.11	1.12	1.11	1.18	0.85	0.69	0.11	1.1
Aeshna	f	0.82	0.87	0.89	1.52	0.15	0.43	0.16	0.9
affinis	h	0.64	1.08	0.96	1.37	0.17	0.19	0.18	0.95
A.	f	1.39	0.9	0.77	1	0.14	0.11	0.21	0.85
bonariensis	h	1.6	0.9	0.8	0.97	0.09	0.45	1	0.93
A.	f	0.66	0.82	0.91	0.93	0.65	0.56	0.98	0.84
cyanea	h	0.84	0.87	0.85	1.22	0.58	0.38	0.67	0.88
A.	f	0.59	0.88	0.77	1.05	0.24	0.5	0.16	0.79
mixta	h	0.9	0.88	0.87	0.99	0.18	0.5	0.33	0.87
Anax	f	0.84	0.79	0.77	1.71	0.25	0.26	0.49	0.81
imperator	h	1.05	0.79	0.81	1.79	0.3	0.26	0.24	0.88
Hemianax	f	1.24	0.99	0.85	1.3	0.16	0.08	0.29	0.94
ephippiger	h	1.44	0.98	0.85	1.31	0.12	0.2	0.43	1.04
Brachytron	f	0.86	0.89	0.92	1.47	0.68	0.67	2	0.96
pratense	h	0.74	0.97	0.94	1.41	0.73	0.59	1.22	0.96
Boyeria	f	0.81	0.81	0.73	1.02	0.34	0.2	1.05	0.79
irene	h	0.6	0.96	0.87	1.13	0.31	0.2	0.82	0.84
Progomphus	f	0.8	0.9	1	1.19	0.3	0.2	0.67	0.95
zonatus	h	1.08	0.79	1.05	1.29	0.29	0.55	0.33	0.97
Gomphoides	f	1.05	0.88	0.95	1.31	0.23	0.4	0.09	0.97
sp.	h	1.11	1.15	0.92	1.24	0.14	0.54	0.13	1.05
Onychogomphus	f	0.66	0.6	0.69	0.75	0.19	0.13	0.38	0.64
forcipatus	h	0.96	0.74	0.79	0.85	0.21	0.28	0.33	0.78
O.	f	0.95	0.83	0.87	1	0.16	0.11	1.67	0.86
forcipatus ♀	h	1.08	0.83	0.83	1.02	0.14	0.47	0.5	0.9

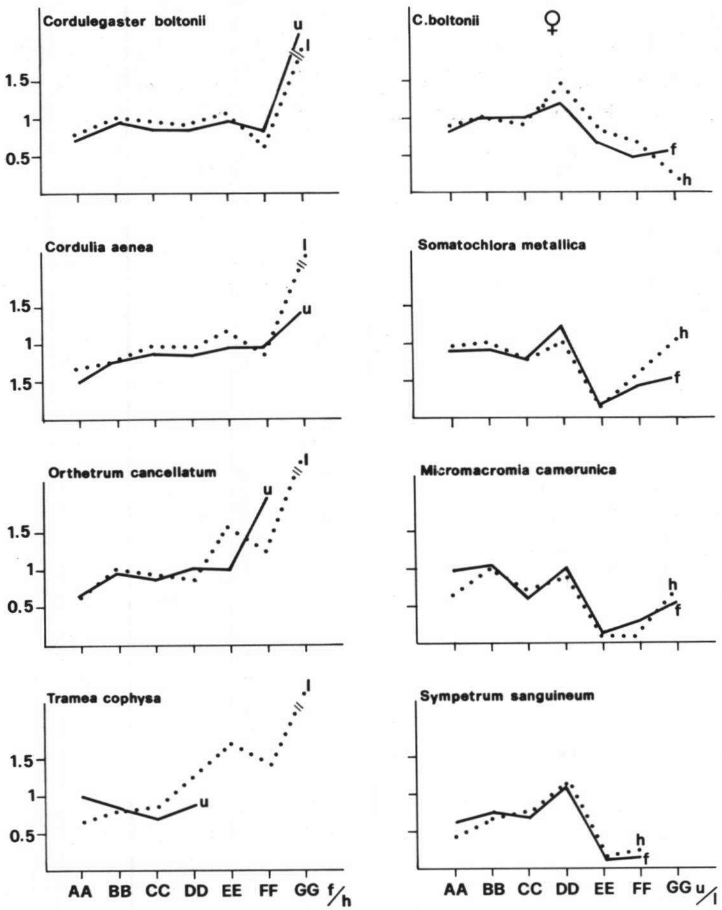

Fig. 3. Ratios between fore/hind (f/h) and upper (u/l) wings in *Cordulegaster boltonii* and some Libelluloidea. — [See Fig. 2 for explanation of the symbols].

field. The cross veins between R and Rs are smooth except for an occasional spine. A few spines appear between CuP and A_1 (basally) and the cross veins of the DC. Spines are longer and more numerous on the Ans and Pns between C and Sc veins and between R_1 and R_2.

Lower surface. — Large Sc spines are present on Sc and CuP veins (basally). Smaller spines occur on the serrated surface of R_2, R_3 (up to but not beyond the Pt) and R_{4+5}(after the first third). The Se spines found in the distal tract in CuP shrink in size towards the margin. Small Sc spines occur on Rs, which does not have a serrated surface, while R_{2+3} are smooth. Among the (+) longitudinal nervures the R, R_1 up to the Pt, the first half of IR_3 and MA are smooth. So is the basal tract of A_1 with the exception of a few L spines which distally increase in number on the branches. The L spines on the cross veins, particularly numerous between R and Rs, are otherwise alike in number and distribution to the overlying Se spines.

Other species studied: *Cordulegaster bidentatus* Selys, 1843 (1 ♂, Italy), *C. princeps* Morton, 1916 (1 ♀, Marocco) (Cordulegastrinae).

Both *C. bidentatus* and *C. princeps* have spurs and very large Sc spines at the base of A_1 on the upper surface of both wings. In the anal field of the fore wing the cross veins have tiny "teeth" (Sc spines), while in the hind wing these have Se spines beginning at the wing base and becoming slightly shorter in the anal triangle, a trait which appeared to be associated with the spurs in Aeshnidae as well. In both wings the upper surface of Sc and Rs veins is always smooth as is the lower surface of R and R_1 (in the tract leading up to the Pt). The upper surface of R_{4+5} has a few L spines except in a male specimen of *C. boltonii* where it is smooth. As usual, the values show that between both wing surfaces the greatest number of spines occur on the hind wing (Tab. II) and the greatest density on the fore wing. The fore/hind ratio gives higher values for the lower surface (Tab. IV, Fig. 3), as was more or less true in Aeshnoidea, with a trend of a minimum in AA and FF, and maximum in GG. The upper/lower values fall within the normal range (Tab. VI, Fig. 3).

CORDULIIDAE

Cordulia aenea (L., 1758)

2 ♂, 1 ♀, Italy

Upper surface. — Large Sc spines are present on R and A_1 (basally). Smaller spines rise from a serrated surface up to but not beyond the Pt on R_1, IR_3, MA and the lower branches of Rspl and Mspl (with brief transition zones at the base). Thinner spines occur on the distal branches of A_1, and particularly on the proximal side of the anal loop in the hind wing. Numerous L spines are present on R_2 (except at the middle which is smooth), R_3, Rspl, Mspl and the distal tract of CuP. A few appear on R_{4+5} after the first third, while Rs is smooth. The fore wing of a male has 1 or 2 L spines on the basal tract of the CuP and proximal to the nodus of the Sc vein. The cross veins have Se spines which are smaller near the margins, particularly at the apex and in proximity to the fore anal field. Instead, there is no thinning out in the posterior anal field though the anal triangle is smooth. A few Se spines are present on the Ans and Pns, mostly between C and Sc veins, R_1 and R_2, and on the cross veins between CuP and A_1 before, and on, that of the DC.

Lower surface. — Large Sc spines occur on Sc vein, Rs, R_{2+3}, the first half of R_1 which thereafter is denticulated, and CuP (basally). Smaller and occasio-

Table VI
Ratios of distribution of the L and Se spines between the upper and lower surface of the same wing in *Cordulegaster boltonii* and in some Libelluloidea. — [See Table III for an explanation of the symbols]

Species		AA	BB	CC	DD	EE	FF	GG	TT
Cordulegaster	f	0.84	1.04	0.89	1.15	0.88	1	0.67	0.94
boltonii	h	0.97	1.13	0.99	1.27	0.93	0.76	0.67	1.04
C.	f	0.82	0.99	0.98	1.16	0.64	0.39	0.47	0.93
boltonii ♀	h	0.86	0.99	0.93	1.4	0.82	0.65	0.26	0.97
Cordulia	f	0.79	0.82	0.85	1.05	0.15	0.29	0.35	0.84
aenea	h	1.13	0.78	0.79	0.97	0.17	0.31	0.2	0.85
C.	f	1.07	1.04	0.72	1.01	0.15	0.42	0.88	0.87
aenea ♀	h	1.54	1.04	0.83	1.14	0.18	0.39	1.43	1.06
Hemicordulia	f	0.86	0.9	0.8	1	0.51	0.53	2.1	0.86
mindana	h	1.06	1.25	0.92	0.97	0.21	0.64	2	1.01
Somatochlora	f	0.88	0.9	0.78	1.21	0.16	0.42	0.5	0.88
metallica	h	0.91	0.99	0.78	0.99	0.15	0.54	1	0.87
Oxygastra	f	0.82	0.9	0.88	1.1	0.11	0.37	0.13	0.87
curtisii	h	1.34	0.86	0.88	1.03	0.14	0.25	1	0.94
Micromacromia	f	0.97	1.02	0.56	1	0.1	0.26	0.5	0.78
camerunica	h	0.66	0.95	0.68	0.85	0.05	0.09	0.33	0.74
Uracis'	f	0.58	0.98	0.89	1.18	0.23	0.67	0.13	0.91
ovipositrix	h	0.87	1.05	0.95	1.19	0.34	0.63	0.17	0.98
Brachymesia	f	0.79	0.59	0.73	0.75	0.02	0.29	0.25	0.67
furcata	h	0.48	0.94	0.45	0.94	0.04	0.14	0.33	0.65
B.	f	0.61	1.07	0.87	1.15	0.02	0.5	0.33	0.68
herbida	h	0.69	0.99	0.9	1.28	0.03	1	-	0.94
Ladona	f	0.48	0.81	0.83	1.1	0.26	0.21	0.08	0.81
fulva	h	0.66	0.79	0.81	1.01	0.15	0.17	0.14	0.79
Orthetrum	f	0.84	0.63	0.7	0.78	0.02	0.24	0.25	0.69
cancellatum	h	0.81	0.65	0.7	0.86	0.03	0.2	-	0.73
O.	f	0.77	.0.68	0.8	1.23	0.02	0.33	0.2	0.82
coerulescens	h	0.5	0.65	0.83	1.05	0.07	0.2	0.5	0.75
Crocothemis	f	0.42	0.66	0.76	0.98	0.13	0.33	0.14	0.71
erythraea	h	0.46	0.77	0.62	0.91	0.08	0.33	0.5	0.66

(Continued Table VI).

Species		AA	BB	CC	DD	EE	FF	GG	TT
C.	f	0.46	0.71	0.73	0.83	0.09	0.23	0.28	0.64
erythraea ♀	h	0.48	0.81	0.81	1.34	0.19	0.42	0.14	0.77
Diplacodes	f	1.05	0.74	0.86	1	0.05	0.25	-	0.86
lefebvrei	h	0.51	0.69	0.79	0.97	0.14	0.2	-	0.74
Sympetrum	f	0.63	0.74	0.69	1.05	0.03	0.1	-	0.72
sanguineum	h	0.35	0.67	0.73	1.01	0.04	0.11	-	0.61
S.	f	0.48	0.77	0.77	0.92	0.02	0.07	0.33	0.7
sanguineum ♀	h	0.36	0.75	0.79	1.05	0.03	0.1	-	0.66
S.	f	0.33	0.64	0.69	0.94	0.03	0.06	-	0.63
striolatum	h	0.37	0.63	0.7	1.09	0.04	0.08	-	0.65
Trithemis	f	0.57	0.7	0.95	1.32	0.03	0.17	-	0.82
annulata	h	0.21	0.83	0.94	1.48	0.04	0.2	-	0.61
T.	f	0.59	0.5	0.81	1.4	0.03	0.5	-	0.71
annulata ♀	h	0.2	0.65	0.86	1.41	0.05	0.5	-	0.53
Perithemis	f	0.68	1.04	0.99	1.67	0.1	0.33	-	1.05
mooma	h	0.57	1.04	1.17	1.37	0.02	0.31	-	0.98
Miathyria	f	0.59	0.87	1.06	1.19	0.04	0.25	-	0.88
marcella	h	0.56	0.89	0.97	1.3	0.33	0.5	-	0.95
Pantala	f	0.85	0.9	0.78	1.1	0.04	0.17	0.13	0.88
flavescens	h	0.53	0.63	0.94	1.14	0.33	0.5	-	0.79
Tramea	f	1.08	1.12	0.98	1.23	0.28	0.14	0.33	1.08
cophysa	h	0.74	1.1	1.23	1.31	0.17	0.2	-	1.11
Tholymis	f	0.65	0.79	0.89	1.12	0.17	1.13	-	0.86
tillarga	h	0.65	1.17	0.91	1.06	0.67	0.75	-	0.93
Macrodiplax	f	0.3	0.79	0.69	1.38	0.25	0.25	-	0.75
cora	h	0.29	0.77	0.76	1.46	0.33	0.5	-	0.72
Selysiothemis	f	0.19	0.65	0.81	1.82	0.25	0.5	-	0.75
nigra	h	0.74	0.84	1.1	1.87	0.5	1	-	1.11

nally thinner spines are present on R_3 (last third) and R_{4+5}, rising from a serrated surface. The Rspl, Mspl, distal branch of the CuP and midrib have Se spines. Several L spines are present on R_1, IR_3, MA and A_1 (distally), while R and the basal tract of A_1 are smooth. The L spines on the cross veins are somewhat fewer in proximity to the anal field, particularly on the fore wing and near the marginal cells of both wings, but otherwise are alike in number and distribution to the overlying Se spines.

Other species studied: *Hemicordulia mindana* Needham & Gyger, 1937 (1 ♂, 1 ♀, Philippines), *Somatochlora metallica meridionalis* Nielsen, 1935 (1 ♂, Italy) (Corduliinae); *Oxygastra curtisii* (Dale, 1834) (2 ♂, Italy) (Gomphomacromiinae).

There are many Se spines in the initial tract on the lower side of R_3 in *S. metallica,* the same zone which in *C. aenea* had much thinner than usual spines. In comparison to the other species, *H. mindana* has very few L spines on the upper surface and the middle part of $R_{4+5}$and distal part of CuP are smooth. The Sc, Rs and R veins are smooth, as usual, and — with the exception of a few marginal spines — so is the R_{4+5}. In all the specimens the lower surface of the R_1 has numerous L spines.

Spines are more numerous on both surfaces of the hind wings but densest on the fore wings (Tab. II). The fore/hind ratio (Tab. IV, Fig. 3) shows a low value for AA and a maximum for GG (with the exception of *S. metallica*). The upper/lower ratio follows the typical trend. In comparison to the preceding families, but like Libellulidae, the values for FF and GG are slightly higher (Tab. VI, Fig 3).

LIBELLULIDAE

Orthetrum cancellatum (L., 1758)

2 ♂, 2 ♀, Italy

Upper surface. — Large Sc spines occur on R+M, R and A_1 (basally). Smaller spines are present on R_1 (up to the Pt which thereafter is smooth) and thinner ones in IR_3, MA, lower branches of Rspl and Mspl (with brief transition zones at the base) and A_1 (distally). Some Se spines occur in proximity to the anal loop. The Sc, Rs, R_3, $R_{4+5}$and midrib are smooth. A few L spines appear on R_2 at the beginning and towards the margin, and distally on CuP. The middle part of Rspl and Mspl is smooth. The cross veins have Se spines, shorter at the margins, particularly at the apex and in the proximal part of the anal field. On the hind wing, the zone adjacent to the membranula is smooth, while the cells up to the anal loop have small S spines which gradually increase in density. A few tiny spines are present on the cross veins between R and Rs, the first 5-6 between Rs and MA and between R_2 and IR_3. The Ans are smooth. The Pns are smooth or corrugated before the Pt. A few spines are present between R_1 and R_2 up to but not beyond the Pt.

Lower surface. — Large Sc spines occur on Sc vein, Rs, R_{4+5} and CuP (basally). Smaller spines appear on R_2 (up to the Pt which thereafter is smooth) and R_3. There are Se spines on the Rspl, Mspl, Cup (distally) and the midrib. Several L spines are present on the R_1, IR_3, MA (after the first third) and A_1 (distally). The other (+) longitudinal nervures are smooth. The L spines on the cross veins are alike in size and distribution to the overlying Se spines. However, the Ans are smooth in the hind wing and have a few spines on the fore wing between C and Sc veins. The Pns have many L spines which are most abundant between R_1 and R_2.

Other species studied: *Micromacromia camerunica* Karsch, 1890 (1 ♀, Congo) (Tetrathemistinae); *Uracis ovipositrix* Calvert, 1909 (1 ♂, Brazil) (Brachydiplacinae); *Brachymesia herbida* (Gundlach, 1889) (1 ♂, Cuba), *B. furcata* (Hagen, 1861) (1 ♂, Brazil), *Leucorrhinia dubia* (Vander Linden, 1825) (1 ♂, Italy) (Leucorrhiniinae); *Ladona fulva* (Müller, 1764) (1 ♂, Italy); *Libellula depressa* L., 1758 (1 ♂, 1 ♀, Italy), *L. quadrimaculata* L., 1758 (1 ♂, Italy), *Dasythemis mincki* (Karsch, 1890) (1 ♂, Brazil), *Orthemis ferruginea* (Fabr., 1775) (1 ♂, 1 ♀ Brazil), *Orthetrum brunneum* (Fonscolombe, 1837) (1 ♂, Italy), *O. chrysostigma* (Burmeister, 1839) (1 ♂, Congo), *O. coerulescens* (Fabr., 1798) (1 ♂, Italy) (Libellulinae); *Acisoma trifidum* Kirby, 1889 (1 ♂, Congo), *Brachythemis contaminata* (Fabr., 1793) (1 ♂, India), *Crocothemis erythraea* (Brullé, 1832) (1 ♂, 1 ♀, Italy), *Diplacodes lefebvrei* (Rambur, 1842) (1 ♂, India), *D. nebulosa* (Fabr., 1793) (1 ♂, Malaysia), *Erythemis acuta* Say, 1839 (1 ♂, 1 ♀, Guyana), *Erythrodiplax umbrata* (L., 1758) (1 ♂, 1 ♀, Brazil), *Neurothemis terminata* Ris, 1911 (1 ♂, 1 ♀, Philippines), *Sympetrum sanguineum* (Müller, 1764) (2 ♂, 1 ♀, Italy), *S. striolatum* (Charpentier, 1840) (1 ♂, 1 ♀, Italy) (Sympetrinae); *Trithemis annulata* (Palisot de Beauvois, 1807) (1 ♂, 1 ♀, Italy) (Trithemistinae); *Perithemis mooma* Kirby, 1869 (1 ♀, Brazil), *P. tenera* (Say, 1839) (1 ♂, 1 ♀, Brazil) (Palpopleurinae); *Miathyria marcella* (Selys, 1857) (1 ♂, 1 ♀, Brazil), *Pantala flavescens* (Fabr., 1798) (1 ♂, Malaysia), *Rhyothemis phyllis* (Sulzer, 1776) (1 ♀, Malaysia), *Tholymis tillarga* (Fabr., 1798) (1 ♂, Malaysia), *Tramea cophysa* Hagen, 1867 (1 ♀, Brazil) (Trameinae); *Macrodiplax cora* (Brauer, 1867) (1 ♂, Somalia), *Selysiothemis nigra* (Vander Linden, 1825) (1 ♂, Italy) (Urothemistinae); *Zygonyx ida* Selys, 1869 (1 ♂, Malaysia) (Zygonychinae).

There are no substantial differences between *O. cancellatum* and the various species of Libellulinae, Sympetrinae and Trithemistinae. The Se spines present in the anal field on the upper fore wing surface progressively decrease in number proceeding towards the wing base where the nervures are usually smooth or barely corrugate. In *T. annulata* the basal half of the zone between the anal loop and wing base is smooth. Instead, the L spines on the lower surface of the anal field gradually increase in number proceeding towards the wing base. While Libellulinae (and also *M. camerunica, U. ovipositrix* and Leucorrhiniinae) have a moderate number of L spines and some smooth marginal nervures, Sympetrinae have more of these spines and no smooth nervures. There is a smooth zone around the membranula in *T. annulata* but thereafter spines are very dense, particularly in proximity to the margin. This zone is defined spatially and the density decreases until reaching values similar to the other species at about the level of the DC and thereafter. In *M. marcella* and other species of Trameinae, Urothemistinae and Zygonychinae the Se spines in proximity to the upper anal field are even smaller and fewer. In the hind wing of *M. marcella* the entire zone proximal to the anal loop is smooth, whith the exception of a very few "teeth" adjacent to the latter. This decrease is less marked but nonetheless present in the other species. In proximity to the lower anal field the distribution of the L spines resembles that of Libellulinae, with moderately numerous spines near the anal loop which become smaller and fewer towards the wing base. The basal zone is smooth except for a dozen large spurs on the nervures adjacent to the base of A_1, not found in other species of Trameinae but present on the anal crossing and basal part of A_1 in Urothemistinae. Similar but somewhat smaller spines occur in *Libellula* spp., but not in other specimens of Libellulidae.

In the lower fore wing of Trithemistinae, Trameinae, Urothemistinae and Zygonychinae the marginal cells of the anal field have dense L spines curved towards the external part of the wing, arranged similarly to those in Lestoidea and some Coenagrioidea. Their hind wing has no such spines. Neither do they appear in the other species of Libellulidae examined, with the exception of *O. ferruginea, Orthetrum* spp. (Libellulinae), *Sympetrum* spp., *E. umbrata,* and *A.trifidum* (Sympetrinae) where there is a hint of these spines.

In all the species examined, with the exception of *Perithemis* spp., which has several small spines, the upper surface of the Sc and Rs nervures is smooth, as is the R_{4+5} in most cases particularly in the hind wing. In a great many species, however, the other upper surface (-) longitudinal nervures have a few L spines but in some the (-) nervures are all smooth, particularly on the hind wing, with the occasional exception of the CuP or R_2 and R_3. This latter character is not linked to particular subfamilies and is subject to interindividual variability (in conspecifics the nervures can be smooth or have a few spines).

The R nervure on the lower surface is smooth, except in *Perithemis mooma* and *P. tenera* where the IR_3, MA and A_1 nervures of the upper surface are denticulate in some tracts, as in Zygoptera which have many small Sc spines, while the rest of the wing has many small Se and L spines. This particular arrangement could depend on the wing size (among the smallest of the suborder) (cf. Fig. 4).

Like Corduliidae, but in contrast to the preceding families, the fore R_1 usually has several spines between the nodus and the Pt while the posterior R_1 has fewer spines and can be smooth. The spines on the posterior wing are sometimes smaller in size and number. The posterior R_1 is constantly smooth in the various species of Trameinae, Urothemistinae and Zygonychinae.

The greatest number of spines occur on both surfaces of the hind wing (Tab. II), while the greatest density occurs on the fore wing. The Libellulidae are distinguished by the lack of spines in the antenodal (G) and postnodal (E, F) fields, with the exception of Tetrathemistinae, Brachydiplacinae, Leucorrhiniinae and Libellulinae where E and F are always present and at least the minimum value of G. Instead, in Sympetrinae, Trithemistinae, Palpopleurinae, Trameinae, Urothemistinae and Zygonychinae the values of G and usually E and F values for the upper surface are always missing (Tab. II). The fore/hind ratio gives a maximum EE and minimum FF on the lower wing surface but also on the upper wing in *L. fulva,* ♂ *C. erythraea,* ♂ *T. annulata,* and *P. mooma.* Otherwise EE and GG had maximum values with respect to the other fields (Tab. IV, Fig. 3). Generally speaking, the upper/lower graphs show a maximum in DD, minimum in EE and an increase in values in F-G (Tab. VI, Fig. 3). A typical zig-zag trend appears in Tetrathemistinae, Brachydiplacinae and Leucorrhiniinae, with an upside down W trend to the graph (minimum AA, CC and EE, maximum BB and DD). In Libellulinae, Sympetrinae, Trithemistinae and Palpopleurinae the graph conforms to that of the other families (BB is lower). High values of BB reappear in Trameinae and Urothemistinae.

DISCUSSION

TREND OF THE TOTAL FORE/HIND AND UPPER/LOWER RATIONS

The means of the total fore/hind ratios for the individual families (Tab. VII) show a greater number of spines on the hind wing, which is not surprising considering its greater size. The value for Neopetaliidae cannot be considered as indicative as only one specimen was examined. In each family the upper mean was less, or at most equal to, the lower mean. Thus, the number of spines is relatively higher on the upper hind wing and lower fore wing. The total upper/lower ratios (Tab. VII) give means less than 1, showing that there are more spines on the lower wing. The higher values for the hind wing indicate a minimum difference.

Table VII
Means of the total fore/hind and upper/lower ratios in each family.

Family	Fore/Hind Upper	Fore/Hind Lower	Upper/Lower Fore	Upper/Lower Hind
Epiophlebiidae	0.99	1.17	0.9	1.07
Petaluridae	0.68	0.92	0.7	0.91
Neopetaliidae	1.04	1.1	1.04	1.1
Aeshnidae	0.83	0.88	0.86	0.92
Gomphidae	0.85	0.93	0.86	0.93
Cordulegastridae	0.89	0.92	0.94	1.01
Corduliidae	0.86	0.92	0.86	0.95
Libellulidae	0.89	0.89	0.79	0.79

RELATIONSHIP BETWEEN SPINE NUMBER, DENSITY AND WING SURFACE

The number of spines is usually greater on the hind wing while their density, with rare exceptions, is greater on the fore wing (Tabs I-II). Dividing the wing surface in size classes, and calculating the mean density of each, reveals a certain increase in density with an increase in surface beginning at an intermediate size group (Tab. VIII). Density begins to increase where the surface is smallest: both *Perythemis mooma* and *Epiophlebia superstes* have minimum surface values and maximum density values. It should be remembered that the values for each class are means and within each class there can be variability (Tabs I-II).

RELATIONSHIP BETWEEN SPINE SIZE, WING SURFACE, CHORD AND EXTENSION

The mean spine size in several species, calculated in the central zone of the fore wing at the level of the nodus, together with the values for wing extension and maximum wing chord (which in the fore wing coincides more or less with the

Table VIII
Means of the spine density (d) for the wing surface classes: fwS, fore wing surface; hwS; hind wing surface.

fwS (mm²)	d Upper	d Lower	hwS (mm²)	d Upper	d Lower
Anisoptera					
			700-800	7.6	8.13
			600-700	8.32	8.6
500-600	7.65	9.32	500-600	5.04	5.51
400-500	7.87	8.37	400-500	5.33	5.52
300-400	5.59	6.23	300-400	5.24	5.78
200-300	5.88	7.4	200-300	5.39	7.19
100-200	5.8	7.78	100-200	7.91	9.36
0-100	9.99	10.41			
Anisozygoptera					
100-200	18.95	20.98	100-200	18.98	17.75

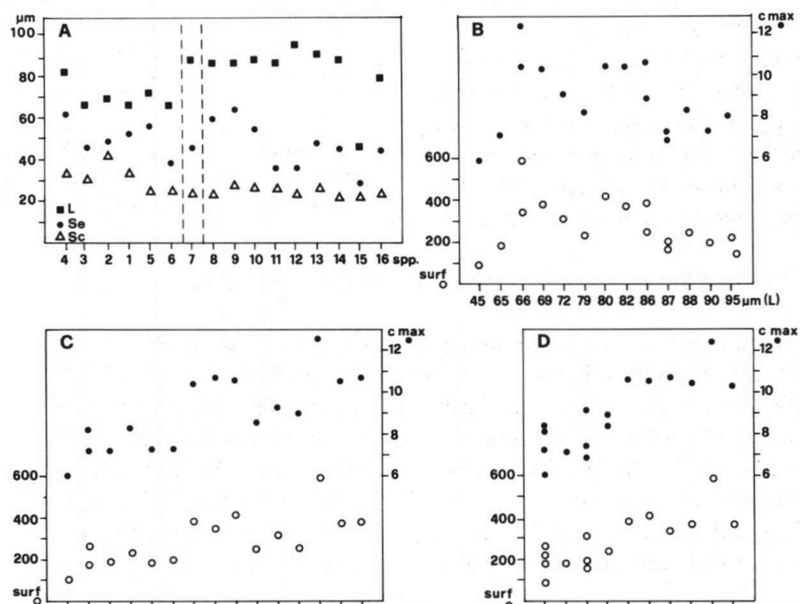

Fig. 4. Wing parameters and spine size. The parameters are listed in Tab. I-II (surface, density) and IX (maximum wing chord, extension). — [A: size of the spines in the species examined: the numbers along the abscissa correspond to those of Tab. IX. — The Super families are separated by the vertical dashed line (L: L spines; — Se: elongate S spines, — Sc: carinate S spines). — B, C, D: variations in the maximum wing chord (cmax) and wing surface (Surf) in relationship to the size of the L, Se and Sc spines respectively].

Table IX
Wing parameters and spine size in some Anisoptera — [L: L spines; — Se: elongated S spines; — Sc: carinate S spines; — cmax: maximum wing chord; — ár: aspect ratio. — The values of spine size, cmax and ar refer to the fore wing]

Species	Spine size (μm) L	Se	Sc	cmax (mm)	ar
Uropetala carovei	66	61	34	12.49	4.95
Phyllopetalia apicalis	69	48	42	10.3	4.5
Aeshna affinis	66	52	30	10.67	3.78
A. cyanea	82	62	33	10.41	4.39
Progomphus zonatus	72	56	25	9.11	4.56
Onychogomphus forcipatus	65	38	24	7.1	4.31
Cordulegaster boltonii	80	53	28	10.51	4.44
Cordulia aenea	86	59	26	8.93	4.01
Hemicordulia mindana	86	64	27	10.63	4.28
Somatochlora metallica	88	54	26	8.35	4.13
Micromacromia camerunica	87	35	25	6.91	4.5
Orthetrum cancellatum	95	35	22	8.12	4.54
Crocothemis erythraea	90	47	25	7.33	4.37
Trithemis annulata	87	44	22	7.16	4.23
Perithemis mooma	45	28	22	5.99	3.17
Miathyria marcella	79	43	22	8.15	4.18

chord at the nodus) is shown in Table IX. The graph of the size trend in S and L spines is shown in Figure 4. The values are closest in the more primitive species and tend to differentiate along the branches leading to Aeshnidae and Libellulidae. The Se spines more or less follow the trend of the Sc spines. The values in *P. mooma* are outside the norm (see below) but both the Se and Sc spines differ from the L spines.

The size of the L spines increases with a decrease in wing surface and chord (Fig. 4B) but only up to a certain point so that some uniformity is maintained. It can be deduced that, within certain limits, large wings have smaller L spines and longer S spines. The preceding hypothesis is supported by Figure 4A as Libelluloidea usually have smaller wings than the other superfamilies. Spine size does not seem to be linked to wing extension, as the latter is more or less constant in all the specimens. The relationship between spine size and density is very uncertain as size should decrease where density is high.

CONCLUSIONS

In Anisozygopyera there are S and L spines with the same morphology as those present in Zygoptera. On the cross veins of the upper wing surface are elongated spines, similar to S spines in distribution and relationship to some wing parameters (Se). In Zygoptera all the upper cross veins have carinate small (Sc) spines except in some of the more primitive species where they are more aciform and where the (-) longitudinals are always spinous. The more recent Zygoptera (including Coenagrioidea) have smooth (-) longitudinals and no Se spines on the upper wing surface. Something similar occurs in the most primitive groups of Anisozygoptera and Anisoptera where the upper surface has cross veins with Se spines and spinous (-) longitudinals, while the more recent groups (such as Libellulidae) have smooth or slightly denticulate nervures in the anal field, wing apex and wing margins, and the (-) longitudinals are often smooth, particularly on the hind wing. As in Zygoptera, the lower surface shows nothing of the kind. It can be hypothesized that this phenomenon is linked in part to the decrease in wing surface. The size of the L spines (most of which occur on the lower wing surface) decreases with a decrease in surface size (Fig. 4). The trend occurs in Zygoptera: minimum spine size is linked to minimum surface in *Chalcopteryx rutilans* as it is in *Perithemis* spp.

Of interest is the variation in mean density of the spines in relation to wing surface, particularly the renewed increase on the lower surfaces. That density increases with the surface was known in Zygoptera, but there the increase in density on the lower surface was not so evident except somewhat on the lower fore wing surface. Correlating size, surface and density leads to the conclusion that large wings have shorter, denser spines, small wings have longer and less dense spines (as in Zygoptera) while tiny dense spines reappear on the smallest wings. The comparison between size and density for the specimens shown in Table IX is less certain, but Table VII gives the mean values for each surface class.

Contrary to Zygoptera, the density of the spines on the upper and lower wing surface of Anisozygoptera and Anisoptera does not conform to their absolute quantity. The fore/hind ratios almost constantly give values lower than 1 (Tabs III-IV) while the density is almost always higher on the fore wing, particularly on the lower surface. Thus Anisoptera have more spines on the hind wing because this is larger, but denser spines on the fore wing. In the specimen of *Epiophlebia superstes* the quantity and density coincide (Tab. I). The individual fields have particular values — the lowest is almost always AA (probably due to the enlarged anal field), EE is often greater than 1 and GG is the highest — indicating a majority of spines on the Ans and Pns of the fore wing. The latter character is marked (with values $\gg 1$) in Zygoptera (Lestoidea, Coenagrioidea) and evidently the fore wing border somehow differs from the other wing zones. The only marked exception to this occurs in *Epiophlebia superstes* where AA shows maximum values (though the hind wing form of the species differs substantially from that of other Anisoptera) and GG minimum values on the lower surface.

The total upper/lower ratios give mean values less than 1 (Tabs V-VI). All the wings have a majority of elongated spines below, particularly the fore wing. The single fields show a constant maximum (often > 1) in correspondence to the fields between R_2 and R_3 (DD) on both wings. In comparison to the other areas of the wing, the Se spines on the upper surface in this zone (immediately posterior to the PT) are more numerous than the lower L spines. Somewhat the same trend appears between R_{4+5} and CuP (BB), though the value is usually much lower than the other with the exception of some subfamilies of Libellulidae (Tetrathemistinae, Brachydiplacinae, Leucorrhiniinae).

No sexual differences appeared between the spine distribution on the fore and hind wings of Anisoptera, in comparison to the surprising differences in some Calopterygidae, Euphaeidae and Chlorocyphidae.

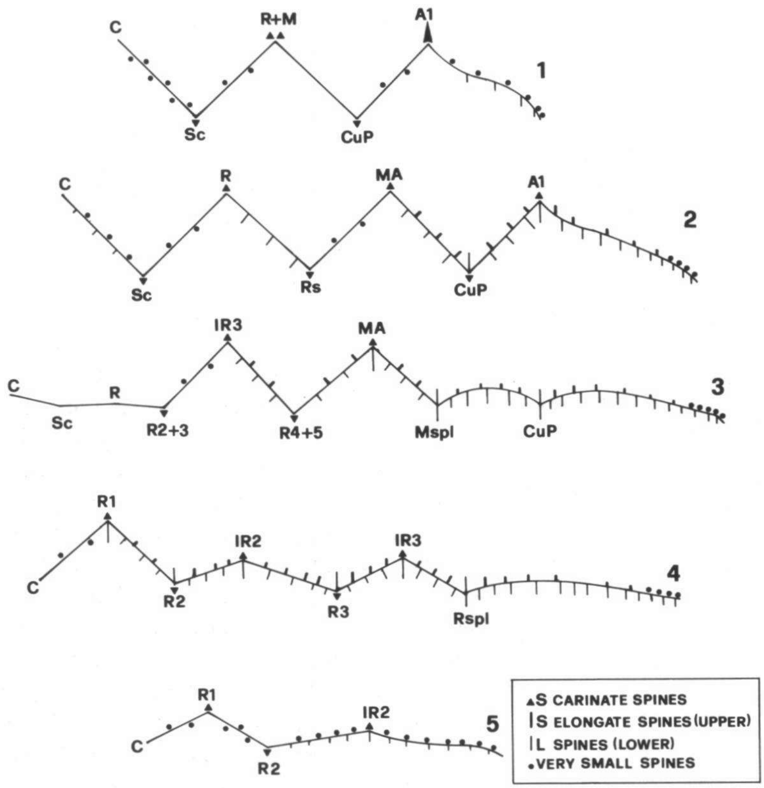

Fig. 5. Section of an Anisoptera wing at various levels: (1) base-DC; — (2) DC-nodus; — (3) nodus; — (4) nodus-Pt; — (5) Pt-apex. — The principal morphological characters of the spines are evident, including the elongated (Se) spines on the upper surface cross veins. Shown are the large Sc spines present on A_1, R and R_1 (upper) and Se spines on Rspl, Mspl and CuP (lower). The greatest number and size of the spines between C and Sc and between R_1 and R_2, as well as the size of the tiny spines at the wing apex, are also given. At the hind margin the L spines (below) are still slightly longer than the Se spines (above). — [For the comparison see Fig. 1].

The distribution and morphology of the spines varies predictably with respect to some nervures or wing zones. The lower surface of the Rspl, Mspl and CuP nervures (and midrib when this is present) have Se spines, though normally the (-) nervures in this area have Sc spines. These latter are present but in smaller numbers and sizes which are intermediate with respect to the others. The Se spines are more numerous on the Mspl and CuP. This size gradient appears on other nervures proceeding from the remigant to the anal fields of the wing. Stubby S spines are present on the Sc, Rs, R_{2+3} and R_2' nervures, smaller and thinner ones on R_3 and R_{4+5}. The spines on the Ans and Pns between Sc and R and between C and R_1 on both surfaces are always smaller and fewer than those between C and Sc and between R_1 and R_2. Thus, in these zones, the position of the spines on the upper and lower wing surface, is inverted with respect to the direction of wing advancement.

In Anisoptera, the upper surface of Sc, Rs, R_{2+3} and the lower surface of R is always smooth. Roughly the opposite is true in *Epiophlebia superstes* which has numerous tiny spines on the Sc and Rs of both wings, like Calopterygoidea. In respect to the rest of the wing, Anisoptera have fewer and smaller spines in proximity to the apex. The spines in the anal field shrink in size proceeding basally in the direction of the DC, less so in the more primitive families and much more so in recent families where the nervures are aften smooth or serrated. The wing apex and bordering zones may or may not have a very few tiny spines. The principal morphological characters cited are summarized in Figure 5.

Within certain limits the spines and characters correlated to these are common throughout the Odonata. Some characters can be linked to large systematic units (suborders, suberfamilies). For example, HEYMER (1973) noted differences with a probable phylogenetic value in the pterostigma of some Polythoridae, Euphaeidae and Calopterygidae. The problem of the function of the spines remains. A working hypothesis is that their presence on the nervures affects the resistance of the wings to stress and strain in preferential points. The spines could have a mechanical function and their different density in certain parts of the wing could be related to different mechanical requirements. Nonetheless, this does not explain the differences in their size and morphology. The spines are substantially longer in the "valleys" of the wing and shorter (and different) on the "crests" or where the membrane flattens out (apex, posterior margin). This fact, together with the particular arrangement of the spines in wing zones important for flight — the leading and trailing edge, apex and zone posterior to the Pt — suggest that they have an aerodynamic function.

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