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SPINES ON THE WING VEINS IN ODONATA. 1. ZYGOPTERA

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The wing veins of Zygoptera are provided with spines which differ morphologically according to whether the vein is convex or concave, and in relation to sex (typically in Euphaeidae, Calopterygidae and Chlorocyphidae) and taxonomic position (distinguishing the more primitive Calopterygoidea from Lestoidea and Coenagrioidea. A certain number of variations are constantly associated with the nodal and cubito-anal spaces of the wings, while size appears to be partially related to the surface area, wing chord and aspect ratio.

INTRODUCTION

In Odonata the wings are not smooth but corrugated due to longitudinals and cross veins, which are spinose on both the upper and lower surfaces. The presence of these spines, which are more or less thickly set and pronounced, can be noted by attempting to slide a piece of paper between a pair of wings folded.

SEGUY (1959) noted that in the wings of *Cordulia aenea* "toutes les nervures sont épineuses". HERTEL (1966) observed the presence of such spines on the two wing surfaces of *Aeshna cyanea,* but did not produce any suggestion as to their aerodynamic function. NEWMAN, SAVAGE & SCHOUELLA (1977) studied the role of the spines in the flight of *Aeshna interrupta* without, however, coming to any clear conclusions. The latter authors measured the length of the spines in *Coenagrion* sp. (60 μm), in *Sympetrum* and *Gomphus* (70-80 μm), and in *Aeshna eremita* and *Anax junius* (100-125 μm). Since no spines were noticed on the upper surface of the *Coenagrion* wings, they have hypothesized that true for the entire suborder (with the possible exception of Lestidae, which do not rest with the wings folded).

The present paper describes the different spines occurring in the Zygoptera, to be followed by the accounts on the situation in the Anisozygoptera and Anisoptera.

MATERIAL AND METHODS

The morphology of the spines was studied with a SEM, and their distribution with a stereomicroscope. The specimens observed with the SEM had to be damaged and thus only a few from each family were used. The distribution of the Calopterygoidea spines was tabulated from a limited number of specimens due to the difficulty in counting thickly set spines on several veins in stained wings.

GENERAL APPEARANCE IN ZYGOPTERA

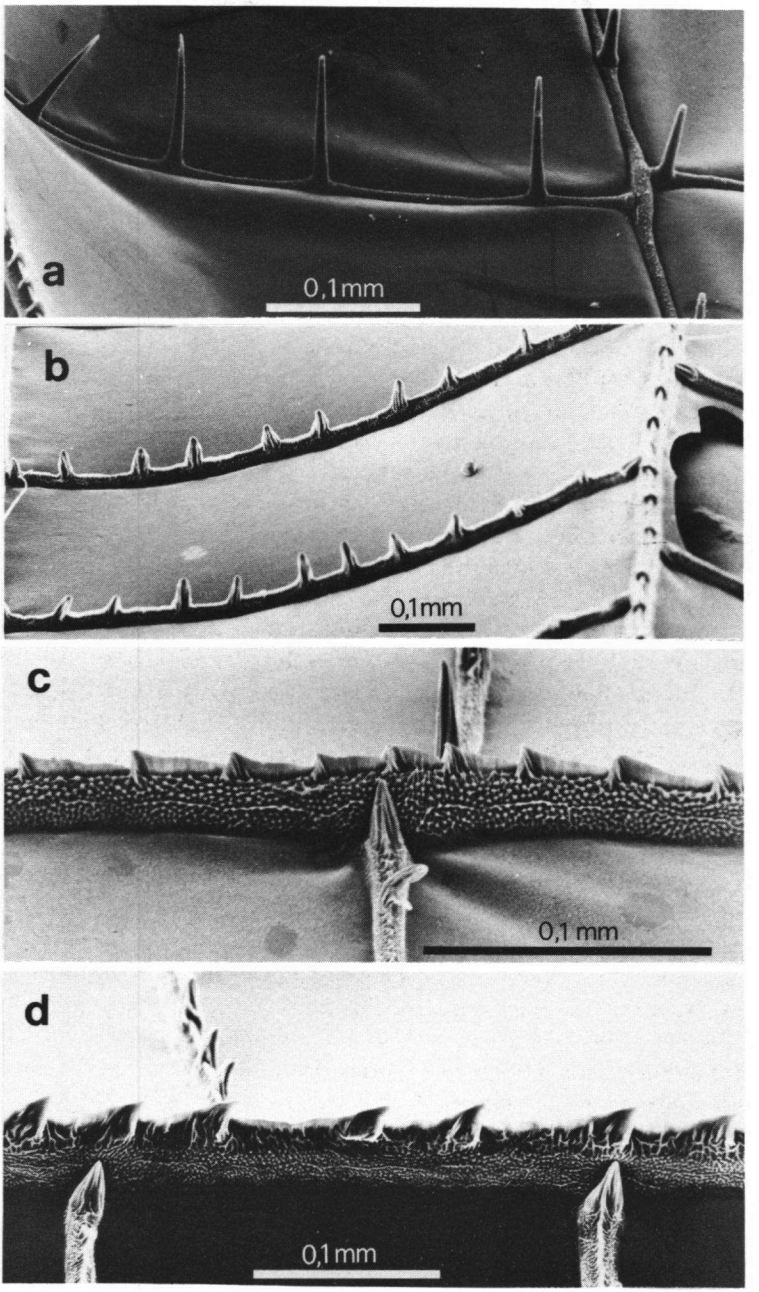
The spines can be divided into two categories: short (S: 8-18 μm) and long (L: 20-70 μm). The former resemble more or less pronounced carinate teeth (Fig. 1c-d; 4; 5), while the latter are grooved cuticular processes which can be elongated and infrequent (40-70 μm; Fig. 1a) or short and closely set (20-40 μm; Fig. 1b). Both categories are present on different parts of the same vein: L on the upper surface of convex (-) and lower surface of concave (+) longitudinals and cross veins, S on the opposite surfaces (Fig. 2). Each vein has a single row of spines, but where veins fuse two parallel rows of spines appear. This is true for the S spines on the upper surface of the R+M on both the fore and hind wings.

Their size changes along the vein: S spines begin at the wing base as tiny excrescences which grow as they approach the distal part of the wing, while L spines first appear after the arculus as well-defined processes which shrink rapidly as they approach the wing margin, where both types are very similar (Fig. 3). The L spines show the greatest variations: in *Platycnemis pennipes,* for example, they vary on the lower wing surface from 51 μm in the zone between R2 and CuP (slightly before the Pt) to 10-20 μm at the wing margin. As the greatest differences appear at the wing margin the sizes reported below refer to means calculated in the central wing zone slightly before, or in an area corresponding to, the Pt.

Intermediate forms appear on the lower wing surface at the origin of the convex intercalary veins (-), where L spines shrink rapidly to the size of S spines (transition zone: Fig. 4). Initially the vein is raised (+) so that the spine morphology seems to follow the type of vein (convex or concave). At the wing margin, where the two types become similar, there is practically no morphological distinction between convex and concave veins.

The number of spines on the wing surface is variable, but a more or less typical quantity appears in each family. A convenient example of this is given by the

Fig. 1. Spine morphology: (a) L spines on IR3 (fore wing, lower surface) of *Ischnura elegans;* — (b) L spines between two intercalary veins midway between the nodus and wing apex (hind wing, lower surface) of *Calopteryx haemorrhoidalis;* — (c) S spines between R2 and R3 (fore wing, lower surface) of *Heteragrion chrysops;* — (d) S spines on R3 (hind wing, lower surface) of *Calopteryx haemorrhoidalis.*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lower wing surface L spines which generally vary less in number between conspecifics than between closely related species or members of the same family (Tabs I-X). However, there is much less interindividual variability in the ratio between the number of L spines in specific zones of the fore and hind wings of conspecific males and females (Tab. XII), (excluding some Calopterygoidea which show sexually-related differences). This datum is also evident from a statistical analysis of *Ischnura elegans* and other species of Coenagrionidae (d'Andrea & Carfì, in prep.).

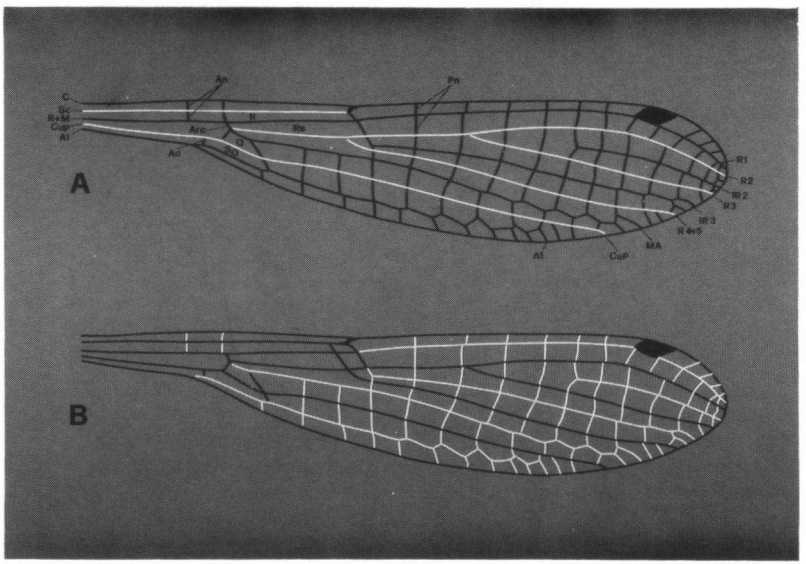


Fig. 2. Distribution of the S and L spines on the wing veins of Zygoptera. — [Black veins: S spines; — white veins: L spines; A: upper wing surface; — B: lower wing surface. The nomenclature is according to TILLYARD & FRASER (1938-1940), except for the family-group names of Megapodagrionidae and Coenagrionidae] — The L spines are usually absent or very rare on the basal part of the wing while they appear in great number along the margin.

At the tip of the cross veins, adjacent to their conjunction with the longitudinals, are spines (Fig. 5) found in all the families examined except Polythoridae. These are most pronounced in the first half of the wing, shrinking towards the tip where they disappear. They generally occur on concave (+) upper surface or convex (-) lower surface veins, but occasionally appear on adjacent veins of both types (Fig. 1b). Their function could be to impede torsion and deformation of the cross veins (altering the valleys and crests of the wing) during flight.

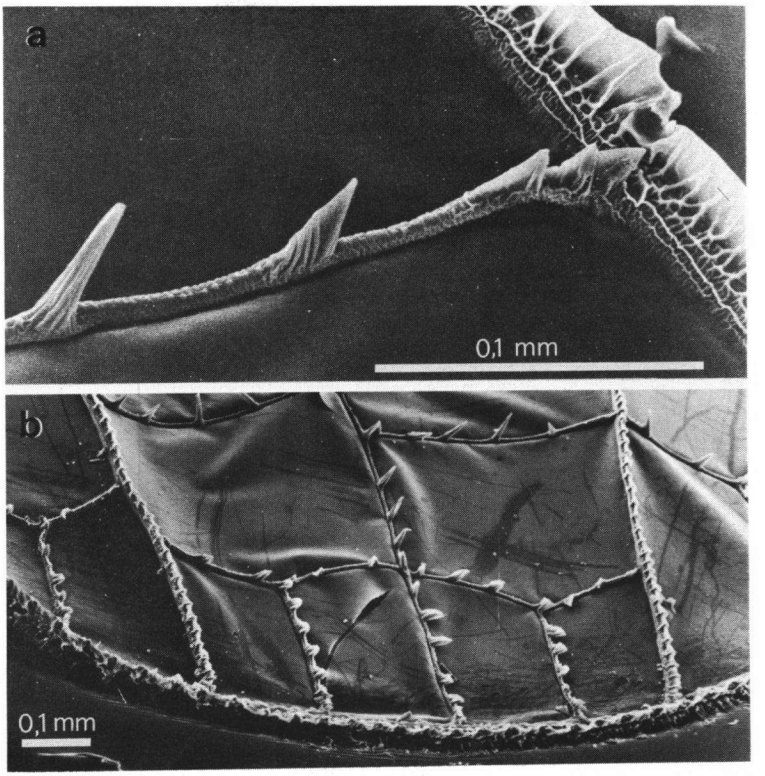


Fig. 3. Size decrease of the L spines along the wing margin. — (a) L spines on the posterior margin (anterior wing, lower surface) of *Platycnemis pennipes;* — (b) L spines on IR2 and adjacent cross veins (fore wing, lower surface) at the wing apex of *Ischnura elegans.*

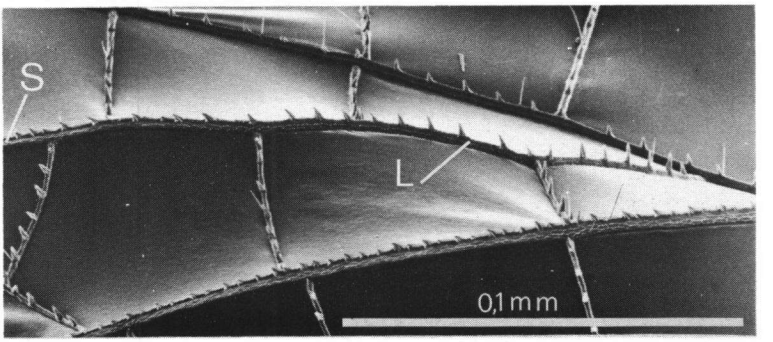
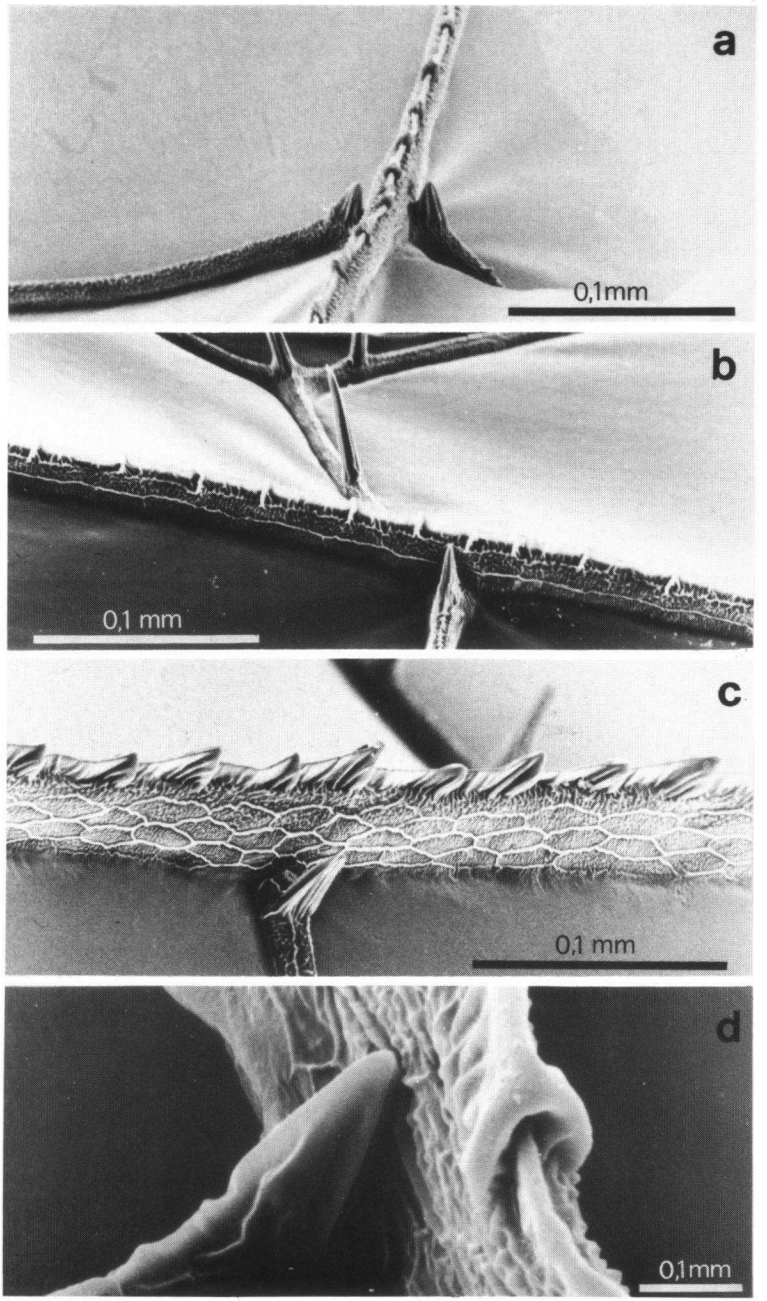


Fig. 4. Transition zone at the base of an intercalary vein (-) on the lower wing surface (hind wing) of *Devadatta podolestoides basilanensis.* — [L: convex surface with L spines; — S: concave surface with S spines]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APPEARANCE IN THE MAIN ZYGOPTERA FAMILIES
POLYTHORIDAE

Chalcopteryx rutilans (Rambur, 1842)

1 ♂, Brazil

Upper surface. — The Sc, R and R1 veins have tiny S spines, while the Ans, Pns, basal cross veins, Q, sQ, and first 6-7 between A1 and the margin are smooth. The remaining cross veins have tiny spines or simple excrescences.

Lower surface. — The (+) and (-) longitudinals are denticulated without any particular differentiation (L, S = 9-10 μm: Fig. 6) though some S spines are slightly more pronounced and thorn-shaped. There are fewer L spines in the anal field and at the hind wing tip than on the fore wing but it was not possible to count them.

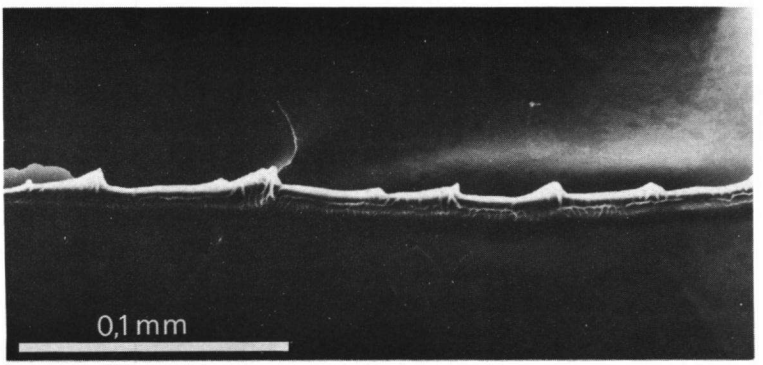

Fig. 6. Spines on a cross vein between R3 and R4+5 (fore wing, lower surface) of *Chalcopteryx rutilans.*

Many archaic traits have been conserved in the larvae and imagoes of the Polythoridae family but not necessarily in the wing spines. Nonetheless, *C.rutilans* is closer to a hypothetically "non-differentiated" form, without any distinctive spine morphology or distribution, than to what has been observed in other families.

Fig. 5. Spines at the conjunction of cross veins and longitudinals: (a) Front view of sector between R2 and R3 (fore wing, lower surface) of *Heteragrion chrysops;* — (b) Side view of R3 (hind wing, lower surface) of *Neoneura amelia;* — (c) Side view of R3 (hind wing, lower surface) of *Devadatta podolestoides basilanensis;* — (d) Side view of R2 (hind wing, lower surface) of *Euphaea amphicyana.*

CALOPTERYGIDAE

Hetaerina rosea Selys, 1853

3 ♂ and 1 ♀, Ecuador

Upper surface. — The (-) longitudinals are smooth or have a few L spines, while the (+) longitudinals have S spines that are closely set and pronounced (R1) or barely visible (IR2, IR3, MA). The Ans and Pns are smooth, while the remainder have tiny closely set S spines, particularly in the distal two-thirds of the wings.

Lower surface. — The (+) longitudinals and cross veins have long (42 μm) L spines in greater concentration on the hind wing (Table I). In the females the fore wings have smooth or only slightly corrugated veins and only slightly pronounced L spines between CuP and R4 + 5 and the Pt. The (-) longitudinals have S spines (12 μm) which shrink towards the margin, smooth Ans, and Pns with a few faint spines at the fore wing tip and along the hind wing margin, some of which are more pronounced. At the beginning of each intercalary vein (-) are typical transition zones.

Also studied were: *Hetaerina macropus* Sel.: 1 ♀,Guyana; — *Calopteryx haemorrhoidalis* (Vander L.): 8 ♂ and 5 ♀, Italy; — *C. splendens* (Harr.): 1 ♂ and 1 ♀, Italy; — *C. virgo meridionalis* Sel.: 4 ♂ and 1 ♀, Italy; — *Vestalis melania* Sel.: 1 ♂ and 1 ♀, the Philippines; — *Phaon iridipennis* (Burm.): 1 ♀, Somalia; — *Mnesarete pudica* (Sel.): 1 ♂ and 1 ♀, Brazil; — *Umma electa* Longf.: 1 ♂ and 1 ♀, Congo.

In all of these, L spines cover all but the basal zone of the lower hind wing and are slightly concentrated on the fore wing. In female *H. macropus* (Tab. I), *V. melania, P. iridipennis* and *M. pudica* (like *H. rosea*) the fore wing has

Table I

Distribution of the L spines on the lower wing surface in some Calopterygidae — [FW: fore wing; — HW: hind wing; — A: field between Cup and posterior wing margin; — B: field between R4+5 and Cup; — C: field between R3 and R4+5; — D: field between R2 and R3; — E: Pns and R1 prior to the Pt; — F: Pns and R1 after the Pt; — 0: smooth or rough veins; — (0): veins with more or less pronounced denticulation but without spines that could clearly be counted (where the spines were longer and visible the value is placed in parentheses)]

Species	Sex and wing	A	B	C	D	E	F	*Total*	
Hetaerina	♂ Fw	98	465	300	372	(6)	(0)	*1235*	(*1241*)
rosea	Hw	296	655	455	359	(59)	(0)	*1755*	(*1814*)
	♀ Fw	0	98	(0)	(0)	0	0	*98*	
	Hw	341	938	645	613	(156)	(0)	*2537*	(*2693*)
	♀ Fw	18	231	205	139	(60)	(0)	*593*	(*653*)
H. macropus	Hw	348	760	552	730	(186)	(0)	*2290*	(*2476*)

some veins with very tiny L spines and others that are smooth. The wings of female *Umma electa* and various species of *Calopteryx* resemble those of the male.

In *C. haemorrhoidalis,* which has a large wing, the spines are closer in size (L=24 μm, S=19 μm) than those in *H. rosea* which has smaller wings. In *Umma electa* the upper surface S spines are scarcer and more pronounced than usual and so similar to the lower surface L spines that looking at the wing in transparency the two surfaces seem to coincide.

EUPHAEIDAE

Euphaea amphicyana Ris, 1930

1 ♂ and 1 ♀, the Philippines

Upper surface. — The (-) longitudinals are smooth while the (+) longitudinals have S spines which are most pronounced on R+M, R1, IR2, IR3 (beginning at the nodus), MA, and A1. The peripheral reticulum is smooth. Some L spines appear on Sc and R2 which are more pronounced on the hind wing. On both wings, the basal part of Sc (up to the first An) and CuP (♂: up to the first An; ♀: up to the arculus) have "pegs" (ca 57 μm, Fig. 7) which are much more numerous in the female (♂: Sc fore and hind 3-4; CuP fore 14-18, hind 15-20; ♀: Sc fore 6-8, hind 13-14; CuP fore 80-82, hind 60-63). The veins are convex so these should be L spines even though they are not grooved. In the female the cross veins are all smooth, while in the male they have a few scattered pronounced S spines (as in *Umma electa*) which are more numerous on the fore wing.

Lower surface. — The hind wing bristles with L spines (38 μm), except for the Ans and Q to sQ cross veins which are smooth. The longitudinals and intercalary veins (+) are full of L spines, including R1 and A1 which have spines up to the wing base. Pronounced S spines are present on Rs, R2, R4+5, and CuP

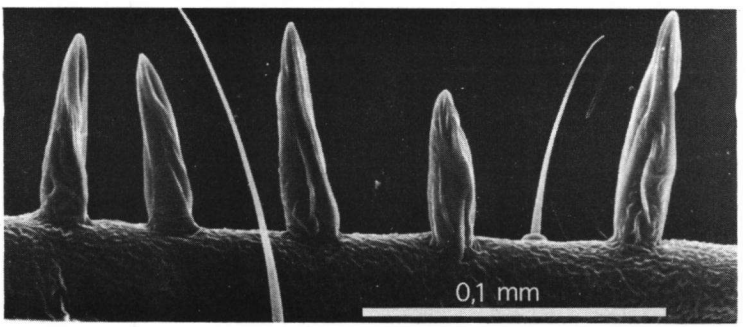

Fig. 7. L spines on the basal part of CuP (hind wing, upper surface) of *Euphaea amphicyana.*

Table II

Distribution of the L spines on the lower wing surface of *Euphaea amphicyana* — [Explanation of symbols in Tab. I]

Sex and wing	A	B	C	D	E	F	*Total*	
♂ Fw	851	847	761	957	(206)	(30)	*3416*	(*3652*)
Hw	742	1001	1067	1614	(191)	(62)	*4424*	(*4677*)
♀ Fw	263	311	235	215	(13)	(8)	*1024*	(*1045*)
Hw	823	861	876	857	(106)	(30)	*3417*	(*3553*)

(after the first fourth), while on the remainder of the wing they are about 11 μm long. The fore wing has fewer and shorter L spines in the female than in the male (15 μm), as in Calopterygidae (Tab. II). The longitudinals and intercalary veins (-) are smooth for about half their length, then S spines appear, some of which become quite pronounced at the margin. The Pn and R1 are particularly smooth. In the male the L spines cover all but the An and cross veins from Q to sQ, while the longitudinals and intercalary veins (+) are smooth for about half their length. There are transition zones at the beginning of each sectorial (-).

Also studied was *Epallage fatime* (Charp.): 1 ♀ Greece.

The fore wing has no L. spines, the veins are at most a bit corrugate, and there are no "pegs" like those at the wing base of *E. amphicyana* were observed.

Calopterygidae and Euphaeidae are generally held to be more closely related to each other than to the other families of Calopterygoidea, and this appears to be confirmed here as well. The convergence is remarkable: the density of the L spines is greater in the hind wing while there are ample variations in the number and size of those on the fore wing, which appear to follow a typical sexual differentiation in many of the species examined. The size of the spines is also comparable.

CHLOROCYPHIDAE

Chlorocypha selysi (Karsch, 1899)

1 ♂, Zaire

Upper surface. — On the fore wing the (-) longitudinal veins bristle with small closely set L spines, some of which are slightly longer in the second half of the CuP and in some of the apical intercalary veins. The (+) longitudinals and cross veins have S spines which become much more pronounced towards the margin. On the hind wing the longitudinals and intercalary veins have a greater number of longer L and S spines. The cross veins are strongly dentate and those between R2 and R3, at the Pt, bristle with thorn-shaped S spines.

Lower surface. — The (+) longitudinals and cross veins have long (46 μm) closely set L spines (Tab. XI) which shrink towards the margin. The R1 and first half of the IR3 are smooth. The (-) longitudinals have S spines (10 μm) which become slightly more pronounced towards the apex. At the fore wing margin the L and S spines are identical in size while at the hind wing margin the L spines are longer. The hind wing Ans and Pns are slightly rugose, the fore wing Ans and Pns a little more so. The L spines are more numerous on the fore wing (Tab. III). At the beginning of the (-) intercalary veins are several transition zones.

Also studied was *Rhinocypha colorata* Sel.: 1 ♂ and 1 ♀, the Philippines.

In the female the lower surface of both wings has fewer and smaller L spines than the male. The most pronounced L spines occur between the MA and the posterior margin.

Sexual dimorphism appears to be more pronounced in Chlorocyphidae (at least in *R. colorata* than in the preceding families. All the wings are involved. The distribution of the L spines between the fore and hind wings is closer to that of Lestoidea and Coenagrioidea.

Table III

Distribution of the L spines on the lower wing surface of male *Chlorocypha selysi.* — [Explanation of symbols in Tab. I]

Wing	A	B	C	D	E	F	*Total*	
Fw	109	331	407	211	(8)	(0)	*1058*	(*1066*)
Hw	111	287	351	169	(4)	(0)	*918*	(*922*)

AMPHIPTERYGIDAE

Devadatta podolestoides basilanensis Laidlaw, 1934

2♂, the Philippines

Upper surface. — The (+) longitudinals have very pronounced S spines, the (-) longitudinals are smooth except at the wing apex, while R2 has L spines from start to finish. The cross veins have well-defined S spines which are densest in the terminal third of the wing. At the apex the S spines are identical in size to the lower surface L spines.

Table IV

Distribution of the L spines on the lower wing surface of male *Devadatta podolestoides basilanensis* — [Explanation of symbols in Tab. I]

Wing	A	B	C	D	E	F	*Total*	
Fw	57	245	735	957	(249)	(162)	*1994*	(*2405*)
Hw	250	613	860	1032	(247)	(171)	*2755*	(*3173*)

Lower surface. — The (+) longitudinals have L spines (39 μm) which are densest from midvein to the margin. The (-) longitudinals have fairly well-defined S spines (14 μm: Fig. 5c). Spines are barely visible on the Ans, while Pns are very spinose from 10a-11a on the fore wing and from 6a-7a on the hind wing. The Q ans sQ cross veins are smooth, while the others have numerous L spines which increase greatly in density along the margin and at the apex of the hind wing. This wing has the largest number of L spines (Tab. IV).

Similar to the preceding families, *D. podolestoides* has fairly small L spines which are most abundant on the lower surface of the hind wing, and fairly long S spines which, on the upper surface, resemble the lower surface L spines. In Lestoidea and Coenagrioidea the upper wing surface is much less "crowded", with smaller S spines (except in Lestoidea) and no or very few L spines. On the lower surface these latter tend to become longer and thinner.

LESTIDAE

Lestes barbarus (Fabricius, 1798)

2 ♂ and 2 ♀, Italy

Upper surface. — The (-) longitudinals are smooth, while the (+) longitudinals, the arculus and all the cross veins (except Ans, and Pns up to and including the Pt) have well-defined S spines which become even more pronounced towards the apex. The R+M and R have small S spines which become more distinct and separate along the R1 vein.

Lower surface. — The (-) longitudinals have well-defined S spines (14 μm) which are most pronounced along the margin. The (+) longitudinals and cross veins have L spines (45 μm) which shrink as they approach the margin and are densest on the fore wing, particularly along the cubito-anal field. The Ans are smooth, while the Pns bristle with tiny spines which after the Pt become more thorn-shaped. There are some transition zones at the beginning of the (-) intercalary veins.

Also studied were *Lestes dryas* Kirby: 1 ♂, Italy; — *L. sponsa* (Hans.): 1 ♂, Italy; — *L. macrostigma* (Eversm.): 1 ♂, Greece; — *L. virens vestalis* Ramb.: 1 ♂, Italy; — *L. tridens* McL.: 2 ♂, Somalia; — *L. uncifer* Karsch: 1 ♂, Somalia; — *L. tenuatus* Ramb.: 1 ♂, Cuba; — *L. forficula* Ramb.: 1 ♂, Cuba; — *L. nodalis* Sel.: 1 ♂ and 1 ♀, Burma; — *Chalcolestes viridis* (Vander L.): 2 ♂ and 1 ♀, Italy; — *Austrolestes* sp.: 1 ♀, Australia; — *Sympecma fusca* (Vander L.): 1 ♂ and 1 ♀, Italy.

In *L. dryas* and *C. viridis* the S spines on some upper surface cross veins are the same size as the L spines on the lower surface. The first two species have a few L spines on the fore wing intercalary vein between IR2 and R3 and on the distal part of R2, while *Austrolestes* sp. have L spines on all the (-) veins. On the lower surface the L spine distribution of these species is similar to that of *L. barbarus* (Tab. V).

Table V

Distribution of the L spines on the lower wing surface of some Lestidae — [Explanation of symbols in Tab. I]

Species	Sex and wing	A	B	C	D	E	F	*Total*	
Lestes barbarus	♂ Fw	231	140	202	99	(51)	(19)	*672*	(*742*)
	Hw	157	124	159	107	(40)	(24)	*547*	(*611*)
	♀ Fw	205	229	206	125	(49)	(25)	*765*	(*839*)
	Hw	96	131	168	115	(17)	(27)	*510*	(*554*)
L. dryas	♂ Fw	274	304	391	251	(94)	(60)	*1220*	(*1374*)
	Hw	192	296	315	203	(69)	(58)	*1006*	(*1133*)
L. forficula	♂ Fw	199	210	194	129	(45)	(31)	*732*	(*808*)
	Hw	76	132	173	102	(40)	(39)	*483*	(*562*)
L. nodalis	♂ Fw	150	148	133	77	(38)	(14)	*508*	(*560*)
	Hw	76	110	140	64	(21)	(12)	*390*	(*423*)
	♀ Fw	202	196	164	88	(19)	(19)	*650*	(*688*)
	Hw	84	140	108	92	(6)	(14)	*424*	(*444*)
L. virens vestalis	♂ Fw	166	194	164	87	(35)	(20)	*611*	(*666*)
	Hw	76	136	137	93	(15)	(25)	*467*	(*482*)
Chalcolestes viridis	♂ Fw	193	336	303	187	(36)	(18)	*1019*	(*1073*)
	Hw	104	212	182	138	(20)	(12)	*636*	(*668*)
	♀ Fw	158	148	201	131	(41)	(13)	*638*	(*692*)
	Hw	72	138	195	125	(34)	(11)	*530*	(*575*)
Sympecma fusca	♂ Fw	225	346	279	192	(28)	(27)	*1042*	(*1097*)
	Hw	127	287	264	196	(4)	(25)	*874*	(*903*)
	♀ Fw	290	306	288	185	(24)	(23)	*1069*	(*1116*)
	Hw	139	291	276	195	(0)	(0)	*901*	(*901*)

MEGAPODAGRIIDAE

Heteragrion chrysops Selys, 1862

1 ♂, Ecuador

Upper surface. — The (-) longitudinals are smooth, while the (+) longitudinals and cross veins have small S veins. The R1 has the same type of spines seen in the Lestidae, and some of the S spines on the fore wing are longer and thorn-shaped.

Lower surface. — The (-) longitudinals have short (10 μm) S spines (Fig. 1c) which are slightly more pronounced at the margin. The (+) longitudinals are

Table VI

Distribution of the L spines on the lower wing surface of male *Heteragrion chrysops* — [Explanation of symbols in Tab. I]

Wing	A	B	C	D	E	F	*Total*	
Fw	90	108	108	114	(0)	(13)	*420*	(*433*)
Hw	80	83	95	110	(0)	(14)	*368*	(*382*)

typically smooth. The Pns are smooth or faintly denticulate, while the other cross veins have L spines (31 μm) which shrink towards the margin. The L spines are more numerous on the fore wing (Tab. VI).

Also studied was *Hypolestes trinitatis* Gundl.: 1 ♂, Cuba.

In *H. trinitatis* (as in some Lestidae) the S spines on some upper surface cross veins are the same size as the L spines. In contrast to what occurs in *H. chrysops*, the spines on the upper surface of R_1 do not become more pronounced.

PSEUDOSTIGMATIDAE

Mecistogaster marchali Rambur, 1842

1 ♂, Surinam

Upper surface. — The (-) longitudinals are smooth, while S spines occur on R, R1, IR2, IR3, MA and A1, shrinking as they approach the margin. The Ans are smooth and the Pns faintly denticulate (the first 7-8 between R1 and R2 are smooth). All the other cross veins have small S spines except just before and under the pseudopterostigma on the cross veins adjacent to the IR2 on the fore wing, where these are unusually large and spur-shaped.

Lower surface. — The veins generally have small L spines (31 μm) which shrink towards the margin. Much longer L spines (51 μm) occur on IR2, MA and A1. The R1 is smooth as is the IR3 almost up to the margin. The (-) longitudinals have well-defined S spines (12 μm). The Ans are smooth. The Pns on the fore wing have several spines after the first 7-8 cross veins, while the hind one is smooth or almost so. The other cross veins have L spines beginning at the mid wing and all over the anal field. These spines are most numerous on the fore wing (Tab. VII).

Table VII

Distribution of the L spines on the lower wing surface of male *Mecistogaster marchali* — [Explanation of symbols in Tab. I]

Wing	A	B	C	D	E	F	*Total*	
Fw	364	421	278	295	(140)	(0)	*1358*	(*1498*)
Hw	304	323	221	295	(11)	(0)	*1113*	(*1124*)

Also studied was *Microstigma rotundatum* Sel.: 1 ♂, Brazil.

This specimen had fewer and smaller spines. On the lower surface the IR2, IR3, MA and A1 are smooth except near the margin of the MA and A1. The Pns are faintly denticulate near the fore wing apex. The other cross veins have very small L spines beginning after the last third of their longitudinals.

PROTONEURIDAE

Neoneura amelia Calvert, 1903

1 ♂, Guyana

Upper surface. — The (-) longitudinals are smooth, except for a few L spines (4-6) on the R2 and R3 near the bifurcation and on the R4+5 at the same level. The (+) longitudinals and cross veins have small S veins which are most evident on R1.

Table VIII

Distribution of the L spines on the lower wing surface of some male Protoneuridae — [Explanation of symbols in Tab. I]

Species	Wing	A	B	C	D	E	F	*Total*
Neoneura amelia	Fw	—	166	111	79	71	5	*432*
	Hw	—	79	69	49	10	7	*214*
N. carnatica	Fw	—	180	143	109	102	34	*568*
	Hw	—	129	131	73	43	15	*391*
Disparoneura quadrimaculata	Fw	82	205	179	118	82	9	*675*
	Hw	35	96	83	74	4	13	*305*

Lower surface. — The (-) longitudinals have S spines (10 μm) which become more pronounced towards the margin. The (+) longitudinals and cross veins have fairly long L spines (48 μm) which shrink as they approach the margin. The spines on R1 are little more than protuberances, but a few are more pronounced. The L spines are most numerous on the fore wing (Tab. VIII). They are particularly crowded on the Pns and on the hind margin cross veins adjacent to the MA as the A1 is reduced. Evidently, the density of the L spines is related to their position on the wing rather than to any particular vein.

Also studied were *Neoneura carnatica* Sel.: 1 ♂, Cuba; — *Disparoneura quadrimaculata* (Ramb.): 1 ♂, India.

Neither specimen has any L spines on the upper surface (-) veins. In *N. carnatica* the lower half of the hind wing R1 is smooth, while it has several L spines on the fore wing. In both species the distribution of the L spines is similar to that of *N. amelia* (Tab. VIII).

PLATYCNEMIDIDAE

Platycnemis pennipes (Pallas, 1771)

3 ♂ and 2 ♀, Italy

Upper surface. — The (-) longitudinals are smooth. The (+) longitudinals and cross veins have S spines which increase in size towards the margin and are present on the Ans and arculus.

Table IX

Distribution of the L spines on the lower wing surface of some Platycnemididae — [Explanation of symbols in Tab. I]

Species	Sex and wing	A	B	C	D	E	F	*Total*
Platycnemis pennipes	♂ Fw	90	94	90	47	9	6	*336*
	Hw	53	63	55	30	1	3	*204*
	♀ Fw	68	81	56	26	7	3	*241*
	Hw	52	43	44	15	1	4	*158*
P. latipes	♂ Fw	61	74	56	32	9	2	*234*
	Hw	32	52	54	28	1	1	*168*
	♀ Fw	82	80	65	37	4	3	*271*
	Hw	54	63	58	31	1	2	*209*
P. hyalinata	♂ Fw	71	92	90	47	8	5	*313*
	Hw	64	57	60	62	1	4	*248*
Copera annulata	♂ Fw	45	134	77	48	59	3	*466*
	Hw	87	84	58	25	3	2	*259*
Risiocnemis incisa	♂ Fw	99	94	78	51	23	11	*356*
	Hw	65	76	76	52	2	16	*287*

Lower surface. — The (-) longitudinals have small S spines (10 μm), which are slightly more pronounced towards the margin. The (+) longitudinals and cross veins have long (54 μm) L spines which shrink rapidly upon reaching the margin (Fig. 3a). The Ans are smooth as are the Pns which, on the fore wing, have a few spines after the mid-wing, between C and R1. The L spines are more numerous on the fore wing (Tab. IX).

Also studied were: *Platycnemis hyalinata* (Brullé): 1 ♂, Madagascar; — *P.acutipennis* Sel.: 1 ♀, France; — *P. latipes* Ramb.: 2 ♂ and 1 ♀, France; — *P. subdilatata* Sel.: 2 ♂, Marocco; — *Risiocnemis incisa* Kimmins: 2 ♂, the Philippines; — *Copera annulata* (Sel.): 1 ♂, India.

There are a few L spines on the fore wing Pns of *R. incisa,* between C and R1 and between R1 and R2. In *C. annulata* these spines appear only at or near

the wing margin on the lower surface (+) longitudinals, except on A1 where they are missing only proximally. The distribution of the L spines resembles that of *P. pennipes* (Tab. IX).

COENAGRIONIDAE

Ischnura elegans (Vander Linden, 1820)

34 ♂ and 7 ♀, Italy

Upper surface. — The (-) longitudinals are smooth except the apical part of R2 which has 1-4 L spines (6 out of 34 ♂, 3 out of 7 ♀) but never on all four wings. The (+) longitudinals and cross veins have S spines which shrink towards the margin.

Lower surface. — The (-) longitudinals have small S spines (9 μm), while there are 3-5 more pronounced spines on the CuP between the arculus and Ac. The (+) longitudinals and cross veins have very long needle-like L spines (70 μm: Fig. 1a). The Ans are smooth, and the R1 usually so except for an occasional (1-3) L spine. On the hind wing L spines occur only between R1 and R2 on the Pns. The spines are most numerous on the fore wing (Tab. X).

Also studied were *Ischnura senegalensis* (Ramb.): 1 ♂, Somalia; — *Enallagma cyathigerum* (Charp.): 1 ♂ and 1 ♀, Italy; — *E. cheliferum* Sel.: 1 ♂, Brazil; — *Ceratura capreola* (Hag.): 1 ♀, Brazil; — *Coenagrion puella* (L.): 1 ♂, Italy; — *Cercion lindeni* (Sel.): 1 ♂ and 1 ♀, Italy; — *Pyrrhosoma nymphula* (Sulz.): 1 ♂, Greece; — *Argia oculata* Sel.: 1 ♂, Brazil; — *Telebasis dominicana* (Sel.): 1 ♂, Cuba; — *T. carmesina* Calv.: 1 ♂, Brazil.

In *E. cyathigerum* the L spines appear on the hind wing Pns between C and R1. In *P. nymphula* the first upper surface cross veins between MA and A1 have some slender S spines which resemble the underlying L spines. The other species do not show any important variations, and none of them have any L spines on their upper wing surface. The distribution of the L spines resembles that of *I. elegans* (Tab. X).

In Coenagrioidea the S spines are quite short (8-11 μm) while the L spines are much longer (<50 μm). These latter are distributed in the same way on the lower surface, and absent on the upper wing surface of all but *Neonura amelia* and *Ischnura elegans*.

CONCLUSIONS

The morphology and distribution of the spines in Zygoptera are summarized in Tables XI-XII, and in Figure 8. The ratio between the size of S and L spines (Tab. XI) and graph of their size trend (Fig. 8A) confirm what appears to the eye: the spines are much closer in size in the more primitive species — typically in Polythoridae and Calopterygidae — than in the other Zygoptera. They tend to diverge greatly in the more recent families of Coenagrioidea. The upper wing surface S spines of some Calopterygoidea and Lestoidea are more pronounced

Table X

Distribution of the L spines on the lower wing surface of some Coenagrionidae — [Explanation of symbols in Tab. I]

Species	Sex and wing	A	B	C	D	E	F	*Total*
Ischnura elegans	♂ FW	91	72	68	52	37	28	*348*
	Hw	50	56	55	36	3	24	*224*
	♀ Fw	113	93	86	48	31	28	*339*
	Hw	92	99	86	49	2	23	*351*
I. senegalensis	♂ Fw	95	101	85	53	57	27	*418*
	Hw	62	76	83	53	9	27	*310*
Enallagma cyathigerum	♂ Fw	215	143	106	81	51	35	*631*
	Hw	149	150	120	100	4	30	*553*
	♀ Fw	145	69	60	34	43	24	*375*
	Hw	112	96	72	51	3	13	*347*
Ceratura capreola	♀ Fw	35	54	43	34	27	10	*203*
	Hw	25	36	37	18	2	6	*124*
Coenagrion puella	♂ Fw	101	94	76	70	55	18	*414*
	Hw	83	62	64	50	3	25	*287*
Cercion lindeni	♂ Fw	124	116	114	74	31	49	*508*
	Hw	90	107	92	66	3	43	*401*
	♀ Fw	186	168	113	81	60	23	*631*
	Hw	145	138	112	65	11	25	*496*
Pyrrhosoma nymphula	♂ Fw	279	256	244	189	71	23	*1062*
	Hw	191	220	207	158	18	24	*818*
Argia oculata	♂ Fw	244	252	224	147	166	11	*1044*
	Hw	132	169	164	89	60	7	*621*
Telebasis dominicana	♂ Fw	101	110	91	44	72	14	*432*
	Hw	61	75	73	41	26	10	*286*

and thorn-shaped, and apparently supplement or substitute whatever is the function of the underlying L spines. This results in a similar morphology of the upper and lower wing surface: furthermore the upper surface (-) longitudinals at times are spinose (L). Exactly the opposite occurs in Coenagrioidea: the S spines are very small, the upper (-) longitudinals are smooth, and the upper wing surface appears "bare"in comparison to the lower one.

The L spines increase in size as the wing chord and surface area diminish (Fig.

Table XI

Spine size and wing shape in male Zygoptera. It was not possible to make accurate counts in *Calopteryx haemorrhoidalis*. — [A "+" sign indicates the wing with the majority of L spines, a "?" indicates uncertainty. Density values are obviously lacking. In *Mecistogaster marchali* the L spines have two values due to the presence of several distinct spines (white circles in Fig. 8c) which are larger than those found on the remainder of the wing. — s. spine size (μm); — N: number of spines; — Surf: wing surface (mm²); — cmax: maximum wing chord (mm); — Ar: aspect ratio; — Fw, fore wing; — Hw, hind wing. — The values of cmax and Ar refer to the wing with a majority of L spines]

Species	s (μm)		sL/sS	N		Surf (mm²)		Density L (N/Surf)		cmax	Ar
	L	S		Fw	Hw	Fw	Hw	Fw	Hw	(mm)	
(1) *Chalcopteryx rutilans*	10	9	1.1	?-	?+	79.21	69.36	-	-	5.40	3.69
(2) *Euphaea amphicyana*	38	11	2.5	3652	4677	288.26	268.42	12.7	17.4	8.69	4.57
(3) *Calopteryx haemorrhoidalis*	24	19	1.3	-	+	357.99	346.52	-	-	11.96	3.07
(4) *Hetaerina rosea*	42	12	3.5	1241	1814	223.33	210.45	5.6	8.6	7.24	4.61
(5) *Chlorocypha selysi*	46	10	4.6	1066	922	120.23	133.33	8.9	6.9	5.09	5.70
(6) *Devadatta podolestoides*	39	14	2.8	2405	3173	206.69	188.76	11.6	16.8	8.80	4.69
(7) *Lestes barbarus*	45	14	3.2	742	611	107.11	93.50	6.9	6.5	5.32	4.85
(8) *Heteragrion chrysops*	35	10	3.5	433	382	103.05	96.97	4.2	3.9	4.67	6.08
(9) *Mecistogaster marchali*	51 31	12	4.3 2.6	1498	1124	582.15	551.53	2.6	2.0	10.60	6.88
(10) *Neoneura amelia*	48	10	4.8	432	214	55.79	60.75	7.7	3.5	3.98	5.23
(11) *Platycnemis pennipes*	54	10	5.4	336	204	117.15	111.20	2.9	1.9	6.11	4.46
(12) *Cercion lindeni*	68	9	7.6	508	401	64.04	54.74	7.9	7.3	3.93	5.55
(13) *Ischnura elegans*	70	9	7.8	348	224	59.02	53.84	5.9	4.2	3.92	4.84

8B, D). The most notable exceptions are *Chalcopteryx rutilans* (L=10 μm; cmax=5.4 mm), whose spines are in many ways distinctive, and *Heteragrion chrysops* (L=35 μm; cmax=4.67 mm). However, only one specimen of each species was examined. The increase in size of the L spines seems at first glance to be inversely proportional to their density (Fig. 8E), but it is not yet known if, and to what degree, the variability in the number of these spines in conspecifics is related to eventual changes in the wing surface. Spine size appears to be more or less independent of the aspect ratio (Fig. 8C). In *Mecistogaster marchali* the aspect ratio exceeds the size of some (31 μm) but not all (51 μm) of the L spines (Fig. 8C, white circle). The S spines, instead, increase in size as the wing chord and surface area increase (Fig. 8F).

The above leads to the conclusion that within certain limits large wide wings have shorter and more numerous L spines and longer S spines than small narrow wings. In *Mecistogaster marchali,* which has large narrow wings, the L spines are smaller and the S spines larger than what would be expected from the wing aspect ratio. However, the dimensions are close to those found in species with comparable wing surface area values. Perhaps surface area is more related to size than to aspect ratio. A statistical analysis of the above traits should provide

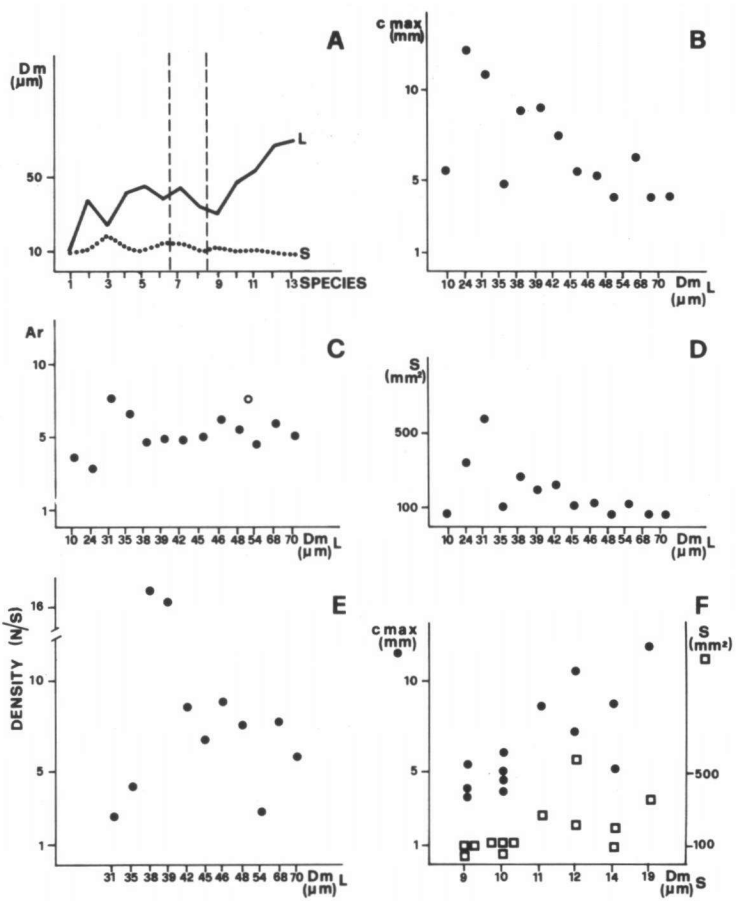

Fig. 8. Wing parameters and spine size. The parameters are those listed in Tab. XI: (A) Size of the spines in the species examined (the abscissae correspond to the numeration in Tab. XI, the vertical dashed lines separate the superfamilies); (B, C, D, E): Variations in the maximum wing chord, aspect ratio, wing surface and density in relationship to the L spine size; — (F) variations in the maximum wing chord and surface in relationship to the S spine size. — [See Tab. XI for the remaining symbols]

the answer to this question which is of interest not only to systematists, and is already being carried out on some species of Coenagrionidae.

The distribution of the L spines between the fore and hind wings (Tab. XII) indicates that Lestoidea and Coenagrioidea form a more or less homogenous group. In all the specimens examined of these two superfamilies the fore wing has the most L spines, while the opposite is true in Calopterygoidea (with the

exception of *Chlorocypha selysi*). The number of L spines is also greater on the cubito-anal space (AA; for *Neonura* spp. BB) — and even more so on the Pns near the leading edge, prior to the Pt (EE). Allowing for a certain variability, this latter datum emerges as being typical of Coenagrioidea.

In contrast to what happens in some species of Calopterygidae, Euphaeidae and Chlorocyphidae (*Rhinocypha colorata*), there is no particular sexual dimorphism in Lestoidea and Coenagrioidea as results from counts made on

Table XII

Ratio of L spine distribution on the lower wing surface of Zygoptera, based on the data of Tables I-X. — [AA, BB, CC, DD, EE, FF, TT: ratio of the values of A, B, C, D, E, F and T (see Tab. I between the fore and hind wing. The 0 values of the preceding Tables are considered as 1 in order to calculate the ratios]

Taxa		AA	BB	CC	DD	EE	FF	TT	
Calopterygoidea									
Calopterygidae									
Hetaerina	♂	0.3	0.7	0.7	1.03	(0.1)	(0)	0.7	(0.7)
rosea	♀	0.03	0.1	0.002	0.001	(0.01)	(0)	0.04	(0.04)
H. macropus	♀	0.1	0.3	0.4	0.2	(0.3)	(0)	0.3	(0.3)
Euphaeidae									
Euphaea	♂	1.2	0.9	0.7	0.6	(1.1)	(0.5)	0.8	(0.8)
amphicyana	♀	0.3	0.4	0.3	0.3	(0.1)	(0.3)	0.3	(0.3)
Chlorocyphidae									
Chlorocypha selysi	♂	0.98	1.2	1.2	1.3	(8)	(0)	1.2	(1.2)
Amphipterygidae									
Devadatta podolestoides	♂	0.2	0.4	0.9	0.9	(1.01)	(0.95)	0.7	(0.8)
Lestoidea									
Lestidae									
Lestes	♂	1.5	1.1	1.3	0.9	(1.3)	(0.8)	1.2	(1.2)
barbarus	♀	2.1	1.8	1.2	1.1	(2.9)	(0.9)	1.5	(1.5)
L. nodalis	♂	1.98	1.4	0.95	1.2	(1.8)	(1.2)	1.3	(1.3)
	♀	2.4	1.4	1.5	0.92	(3.2)	(1.4)	1.5	(1.5)
L. dryas	♂	1.4	1.03	1.2	1.2	(1.4)	(1.03)	1.2	(1.2)
L. forficula	♂	2.6	1.6	1.1	1.3	(1.1)	(0.8)	1.5	(1.4)
L. virens	♂	2.2	1.4	1.2	0.9	(2.3)	(0.8)	1.3	(1.4)
Chalcolestes	♂	1.9	1.6	1.7	1.4	(1.8)	(1.5)	1.6	(1.6)
viridis	♀	2.2	1.1	1.03	1.1	(1.2)	(1.2)	1.2	(1.2)
Sympecma	♂	1.8	1.2	1.1	0.97	(7)	(1.1)	1.2	(1.2)
fusca	♀	2.1	1.1	1.04	0.95	(0)	(0)	1.2	
Megapodagrionidae									
Heteragrion chrysops	♂	1.1	1.3	1.1	1.04	(0)	(0.9)	1.1	(1.1)

(Continued Table XII).

Taxa		AA	BB	CC	DD	EE	FF	TT	
Coenagrioidea									
Pseudostigmatidae									
Mecistogaster marchali	♂	1.2	1.3	1.3	1.1	(12.3)	(0)	1.2	(1.3
Protoneuridae									
Neoneura amelia	♂	-	2.1	1.6	1.6	7.1	0.7	2.02	
N. carnatica	♂	-	1.4	1.1	1.5	2.4	2.3	1.5	
Disparoneura quadrimaculata	♂	2.3	2.1	2.2	1.6	20.5	0.7	2.2	
Platycnemididae									
Platycnemis	♂	1.7	1.5	1.6	1.6	9	2	1.7	
pennipes	♀	1.3	1.9	1.3	1.7	7	0.8	1.5	
P. latipes	♂	1.9	1.4	1.04	1.1	9	2	1.4	
	♀	1.5	1.3	1.1	1.2	4	1.5	1.3	
P.hyalinata	♂	1.1	1.6	1.5	0.8	8	1.3	1.7	
Copera annulata	♂	1.6	1.6	1.3	1.9	19.6	1.5	1.8	
Risiocnemis incisa	♂	1.5	1.2	1.03	0.9	11.5	0.7	1.2	
Coenagrionidae									
Ischnura	♂	1.8	1.3	1.2	1.4	12.3	1.2	1.6	
elegans	♀	1.2	0.9	1	0.9	15.5	1.2	1.1	
I. senegalensis	♂	1.5	1.3	1.02	1	6.3	1	1.3	
Enallagma	♂	1.4	0.95	0.9	0.8	12.8	1.2	1.1	
cyathigerum	♀	1.3	0.7	0.8	0.6	14.3	1.8	1.1	
Ceratura capreola	♀	1.4	1.5	1.2	1.8	13.5	1.6	1.6	
Coenagrion puella	♂	1.2	1.5	1.2	1.4	18.3	0.7	1.4	
Cercion	♂	1.4	1.1	1.2	1.1	10.3	1.1	1.3	
lindeni	♀	1.3	1.2	1.01	1.2	5.5	0.9	1.3	
Pyrrhosoma nymphula	♂	1.5	1.2	1.2	1.2	3.9	0.95	1.3	
Argia oculata	♂	1.8	1.5	1.4	1.6	2.8	1.6	1.7	
Telebasis dominicana	♂	1.7	1.5	1.2	1.1	2.8	1.4	1.5	

various species (Tabs V-X). The variations between males and females are not constant and can be reversed. If there is a tendency towards sexual dimorphism this will appear only after a greater number of representatives of each genus or species will have been studied.

The distribution of the S and L spines is fairly uniform on both wing surfaces: their number is greatest from the nodal zone distally, at the leading edge, and at the apex and anal regions. These areas are important for flight and support

NEWMAN's et al. (1977) hypothesis that the spines have an aerodynamic function.

The rigidity and strength of the veins with spines may differ from those without these processes, which may provide points of flexion along the longitudinals and maintain the curve of the cross veins. If so, their distribution is related to the stress put on various parts of the wing during flight. Both an aerodynamic and a mechanical function are probably involved.

It is known that during flight the wings of *Calopteryx splendens* are slightly out of phase, that the hind wing beats slightly before the fore one, while in Lestidae the wings are completely out of phase (MAGNAN, 1934; AGUESSE, 1968; RUDOLPH, 1976). The S and L spines of Calopterygidae may be related to the mechanics of *C. splendens* flight (and presumably of the other members of this family), as they may be to the flight of Lestidae, where they have a different morphology and distribution. The hypothesis can be applied to the flight of Euphaeidae and Amphipterygidae which may fly more or less like Calopterygidae. An exception could be Chlorocyphidae, which have parameters similar to the other superfamilies.

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