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THE FLIGHT OF THE RELICT DRAGONFLY *EPIOPHLEBIA SUPERSTES* (SELYS) IN COMPARISON WITH THAT OF THE MODERN ODONATA (ANISOZYGOPTERA: EPIOPHLEBIIDAE)*

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The flight of *E. superstes* was filmed in Japan with a high-speed camera, at up to 500 frames/s. The wingbeat frequency of flying individuals is 40-52 Hz. Always with the fore- and hindwings counterstroking, they can both hover and move in all directions and the forward flight is very rapid (up to 9 $m.s^{-1}$ measured). The flight parameters and the orientation of the long axis of the body with respect to flight direction and stroke direction were compared with those of Zygoptera and Anisoptera. *E. superstes* was found to be intermediate between the 2 suborders. With regard to maximal flight speed and flight manoeuvrability it is clearly inferior to modern Anisoptera. The observed direction of the wing stroke relative to the flight path raises aerodynamic questions. These are discussed along with other aspects of flight technique, functional morphology, ecology and phylogeny that bear on the occurrence of *E. superstes* as a relict sp.

INTRODUCTION

The extant Odonata are divided into three suborders, viz. the Zygoptera, the Anisoptera, and the primitive Anisozygoptera (ST. QUENTIN & BEIER, 1968). There are several thousand extant species of each of the first two suborders, but only two anisozygopteran species are in existence today, both of the genus *Epiophlebia*: *E. superstes* (Selys) in Japan and *E. laidlawi* Tillyard in the Himalaya (ASAHINA, 1961).

The Anisozygoptera exhibit morphological characteristics of both suborders. The almost identical fore- and hindwings are similar to zygopteran wings, but

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* Dedicated to Dr S. ASAHINA, for his 80th birthday

the shapes of the body and its anal appendages, as well as the form of the larvae, are more like those of the Anisoptera (ST. QUENTIN & BEIER, 1968). Whether *E. superstes* also resembles both of the other suborders in its behaviour is unknown, as hardly any behavioural observations have been published. The literature includes studies on morphology (ASAHINA, 1939, 1954), larval ecology (ASAHINA, 1939; EDA, 1964; TABARU, 1984) and on egg laying (ASAHINA & SUGIMURA, 1981; TAMIYA & MIYAKAWA, 1984). Only ASAHINA (1950) makes some general remarks about the occurrence and behaviour. Very little, therefore, can be said about the features that adapt *E. supterstes* to its niche, and without such information it is impossible to understand how these apparently ancient dragonflies have managed to persist relatively unchanged for more than two hundred million years, in face of the competition of their modern relatives. Flight analyses can help to clarify the ecological fitness of dragonflies and the principles by which adaptation is brought about. Such studies are especially useful when they are carried out in the field, for it is only there that these easily disturbed dragonflies display their full abilities (RÜPPELL, 1989).

MATERIAL AND METHODS

The flight of *E. superstes* was observed and photographed at the end of April 1991 in Nakamura (Shikoku, Japan) and from the beginning to the middle of May in the mountains at Lake Biwa near Kattata (Shiga prefecture).

The camera was a LOCAM Model 51 with a Kern Switar 16-100 mm lens; Fuji Highspeed 27 DIN film was used, at up to 500 frames/sec. At Katata, feeding flights were filmed from the passenger basket of a mobile crane. Single frames were examined with a NAC Model DF 16B. Wing-surface areas (3 animals) were determined with the geometric-analysis computer KONTRON Videoplan. The weights of 4 animals were measured by K. Inoue, Osaka, 1992. These two sets of data (obtained from different animals) were used to calculate the wing loading. The morphological dimensions of the Anisozygoptera were taken from the literature (ISHIDA et al., 1988) and compared with values for European species given by RÜPPELL (1989). The maximal flight speeds were found by measuring the distances with respect to fixed background features, taking the body length of the animals as a reference. The elapsed time was marked with light-marks on the film at intervals of 0.01 s. These time marks were also used to determine wingbeat frequency.

The non-dimensional flight velocity is defined by ELLINGTON (1984a, 1984b) as the ratio of the distance travelled during one wingbeat to the length of the forewing. The advance ratio was found by dividing the flight speed by the mean stroke velocity (halfway along the wing in the middle of the downstroke). To determine the phase relationship between the paired forewings and the paired hindwings, and the relative durations of upstroke and downstroke, several measurements were made of the anterior and posterior reversal points of the wing movements. All descriptions of stroke paths apply to the forewings, the movements of which are generally easy to discern. The angle of the hindwing stroke path is about 5-10° less than that of the forewing.

E. superstes is a medium-sized dragonfly; in the length of the abdomen (males: 38-40 mm, females: 36-38 mm) and of the wings (males: forewing 33 mm, hindwing 30 mm) it corresponds to small Calopterygidae and other larger Zygoptera or medium Anisoptera of Japan. It is relatively heavy (weight of one male: 285 mg; one female: 385 mg) so that, given the relatively small area of its wings, its wing loading is very large (Tab. I).

The flying season of *E. superstes* in a given area lasts only a little more than two weeks. The time of year depends on the latitude, ranging from the middle of April in the South to the middle of June in the North (ASAHINA, 1950). The females lay eggs in the stems of *Petasites japonicum* (Compositae) which appears early in the year, or in moss (ASAHINA & SUGIMURA, 1981; ASAHINA & EDA, 1958). For comparisons of flight characteristics of the three suborders, material previously published by RÜPPELL (1989) was re-examined. Additional data were obtained from films made in southern France in 1990 (*Sympetrum depressiusculum*) and in Japan in 1991 (*Mnais navaii*).

The Calopterygidae, generally considered as belonging to the Zygoptera, are treated separately in this paper.

RESULTS

GENERAL OBSERVATIONS ON FLIGHT

As a general rule, the flight of *E. superstes* is extremely rapid and straight. Because they often fly in the shade, some practice is required to detect these dragonflies.

When searching for food *E. superstes* flies at high speed in clearings, along woodland paths, over brooks or high in the treetops. The flight path often curves, especially when the dragonflies are examining twigs, while hovering flight is rare during feeding. Having hunted round a tree, *E. superstes* accelerates in a swift, straight downward flight and then ascends again to search near the upper parts of other trees. Alternatively, on leaving a tree it may glide for a while over distances of up to five meters.

From hovering *E. superstes* is able to land on a twig by grasping the leaves. From fast flight, landing on the ground is more like a crash. In one case, after having crashed into the grass just before us, it took more than twenty minutes to start again. In order to mate, the males look for females just above the surface of a mountain stream, covering long distances in rapid straight flight. The females, too, often travel considerable distances in search of suitable substrates for egg-laying.

WINGBEAT FREQUENCIES

The most striking feature of the flight data in Table I is the high wingbeat frequency, which could reach 52 Hz. All the Zygoptera for which this variable has been measured, and the great majority of Anisoptera, beat their wings at a distinctly lower rate. Only very much smaller Anisoptera exceed *E. superstes* in this respect; for example, the American *Perithemis tenera* has a wingbeat frequency as high as 70 Hz.

Table I

Morphological dimensions (for comparison and because of availability range of variation of the Japanese [Ja] and European [Eu] species) and exemplary flight data of Odonata. The flight data for Zygoptera were obtained from *Lestes viridis*, for Calopterygidae from *Calopteryx splendens* and *C. virgo*, and for Anisoptera from *Aeshna cyanea*, all in rapid, straight forward flight (combined from RÜPPELL, 1989). – [N.m^{-2} = Newton . m^{-2}; – *Hz = wingstrokes/s;* – Non-dimensional flight velocity = ratio of the distance travelled during one wingbeat to the length of the forewing; – Advance ratio was found by dividing the flight speed by the mean stroke velocity]

Feature	Sex	*Epiophlebia superstes*	Zygoptera excl. Calopt.	Calopterygidae	Anisoptera
Length abdomen mm	♂	38-40 Ja	15-42	37-64	11-76
	♀	36-38 Ja		33-60	10-86
Weight mm	♂	285 Eu	33-36	92-143	90-894
	♀	385 Eu	40-94	103-186	82-?
Length forewing mm	♂	33 Ja	9-29	30-54	13-60
	♀	Eu	22-27	30-36	25-50
Area of all wings mm^2		602 Eu	190-420	830-1220	680-2300
Wingloading mg.mm^{-2}		0.47 Eu	0.12-0.22	0.11-0.16	0.1-0.59
N.m^{-2}		4.6	1.2-2.16	1.08-1.57	0.98-5.8
Wingbeat frequency Hz		40-52 Eu	33	10.7-19.2	29-46.4*
		(E. superstes)	*(L. viridis)*	*(C. virgo, C. splendens)*	*(A. cyanea)*
Stroke amplitude(*) Forward flight		67-97	117	110	90
Max. flight- -velocity m.s.$^{-1}$		9	2.8	2.2	>10
Flight distance per wingbeat mm		220	45	175	250
Non-dimensional flight-velocity		6.6	1.9	5.7	4.7
advance ratio		4.36	0.8	3	3.42
Phase shift(°) (*) Fore-/hindwings		180	160	18	90
Stroke ratio up:down		1:1	1.5:1	1:1.7	1:1.3

(*) Phase-shift (in degree: 180 = counterstroking; (°) = parallel stroking of hind- and forewings) and stroke amplitude of Anisoptera can be varied largely. – Phase-shift of Calopterygidae is for all flight types excl. courting flight. – Wingbeat frequency from all analysed manoeuvres, other flight parameters from fast forward flight. * excl. the smallest libellulids as *Perithemis* or *Nannothemis* which reach up to 70 Hz.

VELOCITIES

Another conspicuous characteristic is the measured high flight speed, 9 $m.s^{-1}$, which is in the range of anisopteran speeds. It is likely that *E. superstes* can fly even faster for brief periods, since the measured flight was a normal, rapid straight flight along the course of a stream.

Although the distance travelled per wingbeat was measured only for such normal flight, this velocity is greater than in other groups except in Anisoptera (Tab. I); accordingly, so are the parameters calculated from it: the advance ratio (flight speed divided by the mean stroke velocity) and the non-dimensional flight velocity, defined as the ratio of the distance travelled during one wingbeat to the length of the forewing.

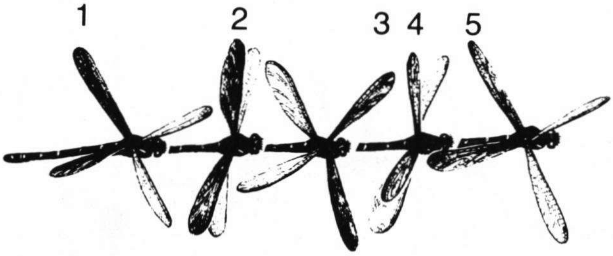

Fig. 1. *E. superstes* flying straight forward (from left to right). The two pairs of wings are beaten a half-cycle out of phase (counterstroking). The numbers above the forewings (dark shaded) identify the consecutive positions of one pair of wings.

PHASE RELATIONSHIPS

With one exception, *E. superstes* flew by counterstroking; that is, the beat cycles of fore- and hindwings were shifted by a half-cycle, so that whenever one pair of wings moved down, the other was moving up (Fig. 1). In only one case, during a backward flight manoeuvre, were one or two beats observed in which the wings moved in synchrony. Synchronous wingbeats were also observed only once in the great number of flight manoeuvres examined for the zygopteran *Lestes viridis*.

In some Calopterygidae, in the giant *Megaloprepus coerulatus* and probably in other Zygoptera and Anisoptera with coloured wings, all four wings usually beat in synchrony. The most varied wingbeats are found in Anisoptera; these can move the wing pairs 180° out of phase (counterstroking), with intermediate phase shifts or, during steep upward or backward flight, in synchrony (RÜPPELL, 1989).

CURVING FLIGHT

Another characteristic of the flight of *E. superstes* is the straightness of the path. During rapid forward flight only very large-radius turns in the range of meters were observed (Fig. 2). The situation is different in the Zygoptera, the Calopterygidae and even in the Anisoptera. Although Zygoptera and Calopterygidae cannot reach such high velocities, even in rapid forward flight they can turn almost on the spot, with one or two wingbeats. The Anisoptera (as observed in *Anax imperator*; RUPPELL, 1989) can also change flight direction very abruptly. To do so, they switch from a phase-shifted to a parallel mode, and probably at a sharp angle of attack, both pairs of wing move simultaneously downwards. Furthermore, the wings on the inside of the curve can briefly tilt to a negative angle, so that they are rapidly pushed downwards by the airstream striking them from above.

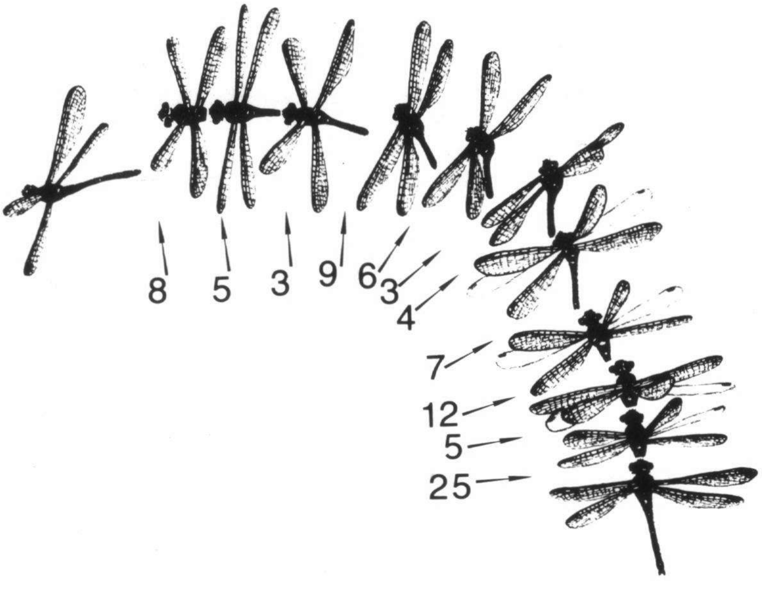

Fig. 2. Curving flight has a large radius. The numbers indicate the frames elapsed between each of the illustrated phases. This slow flight was filmed at 340 frames/s, so that the intervall between two consecutive frames corresponds to 1/340 s = 0.0029 s. The wing outlines drawn in some of the pictures show the starting positions before the following upstroke. The wings on the outside of the curve are beaten further upwards than those on the inside.

In all circumstances, even in curving flight, *E. superstes* beats its wings with counterstrokes (180° out of phase). It adjusts to curving flight by setting the inner wings at a larger angle of attack (always the angle between wing plane and stroke path) and beating the outer wings with a larger stroke-amplitude than the inner wings (Fig. 2). Despite these adjustments, no turn was found to be accomplished with fewer than four wingbeats.

In straight forward flight, too, there are large differences between the groups.

ANGLE BETWEEN THE STROKE PATH AND THE HORIZONTAL OR THE LONG AXIS OF THE BODY

The angle of the stroke path with respect to the long axis of the body is an indicator of the distance above or below the body to which the wingtips can move. These angles were measured for all the manoeuvres investigated, and are shown in Figure 3 to document the differences between the suborders. In the convention used here, the angle is negative when the stroke path is tilted forward and down with respect to the reference axis (here the body axis). The range of variation was greatest in the Anisoptera, and their mean stroke direction was angled most steeply downwards. The mean stroke path of *E. superstes* slanted down less steeply; the angle with respect to the body axis was still less in the Zygoptera. The comparison also shows that the range of the angles of the wing-stroke relative to the long axis of the body was smallest in *E. superstes*.

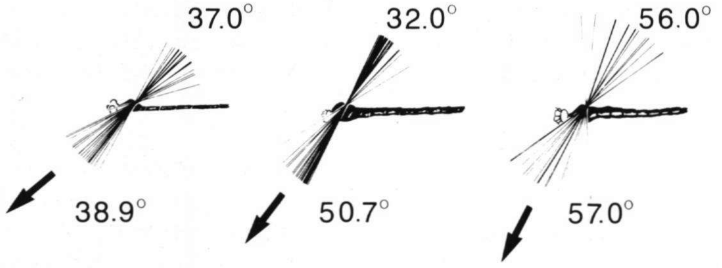

Fig. 3. The stroke directions, with respect to the long axis of the body (shown horizontal in the figure), during various flight manoeuvres (except curving flight) of the zygopteran *Lestes viridis* (left), of *E. superstes* (middle) and of Anisoptera (*Orthetrum, Leucorrhinia, Aeshna, Anax*, right). The angles above the drawings, also presented by the arrows, give the average stroke direction; those below give the variation range of all angles.

The angle between the stroke planes and the horizontal indicates the orientation of the wing stroke in space and hence is informative aerodynamically, especially in relation to the flight direction. Here, again, *E. superstes* is in a separate category, with a stroke path that was relatively similar during flight in all directions (Fig. 4). During forward flight and in all upward flight manoeuvres, including up-and--back, the measured angles were negative (stroke path forward and down). The values for *E. superstes* in all these manoeuvres ranged from -13° to -42°. Only

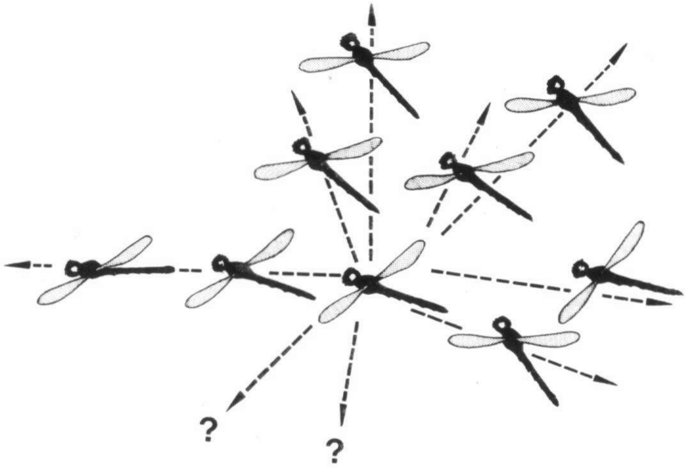

Fig. 4. Spatial orientations of the stroke paths of *E. superstes*. (In each drawing the forewings are shown at the anterior and posterior reversal points) during various flight manoeuvres. The arrows show the flight direction in each case. Flight directions with questionmarks could not be analysed.

during horizontal backward flight did the stroke angle exceed this range, reaching -56°. In the zygopteran *Lestes viridis* the corresponding angles were in the range between -30° and -50°. In the Anisoptera much larger angles were found, from -35° to -83°.

ANGLE BETWEEN LONG AXIS OF BODY AND FLIGHT DIRECTION

In the Zygoptera, the attitude of the body with respect to the flight direction is extremely variable, with angles ranging over 120° C (not including backward flight), from -75° to +45° (here a negative angle signifies that the long axis of the body is pitched up relative to the flight path). The Anisoptera usually keep their body axis aligned with the flight direction, except for the rare upward and backward manoeuvres involving synchronous strokes of both wing pairs (RÜPPELL, 1989), in which values between 115° and 145° are reached.

In *E. superstes* the body angle with respect to the flight direction was in the range -20° to +82°; during rapid forward flight the body was approximately parallel to the flight direction, as in the Anisoptera.

VERTICAL TAKE-OFF

In Figure 5 the vertical take-offs of four species are compared (all in windless conditions, temperature at the take-offs of *Sympetrum depressiusculum* and *Orthe-*

trum cancellatum was around 24°C and about 6-8°C higher than in the other two cases). The calopterygid *Mnais navaii* was very efficient, ascending more than 5 cm with almost one and a half wingbeats in 0.08 s. *S. depressiusculum* performed four wingbeats in the same period and rose even to 10 cm. In contrast, *E. superstes* beats its wings almost 3 times in 0.08 s to achieve an altitude of barely 0.5 cm.

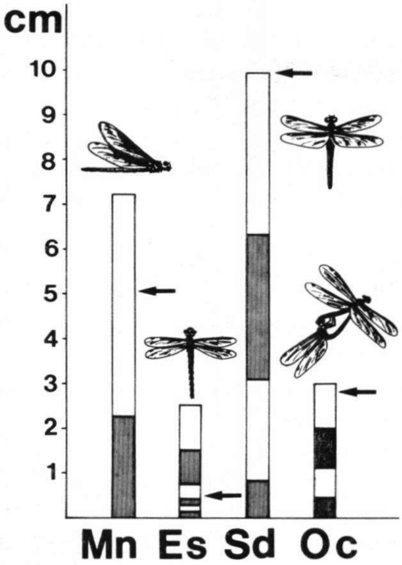

Fig. 5. Comparison of the vertical take-off of *Mnais navaii* [M.n.], *Epiophlebia superstes* [E.s.], *Sympetrum depressiusculum* [S.d.] and *Orthetrum cancellatum* [O.c.] (in mating position). The columns show the number of strokes (each grey or white section shows a stroke, numbers in circles = first and last stroke) needed to travel the distance shown on the ordinate (in cm). Thick arrows mark the distance covered in 0.08 s.

Furthermore, *E. superstes* took a long time to prepare for take-off; it executed 22 wingbeats before the body axis from hanging vertically reached a horizontal position (after a long warm-up period before that with wing-buzzing). Then its legs left the substrate and it became airborne. The other species examined began to fly with the very first stroke. After *E. superstes* had be-

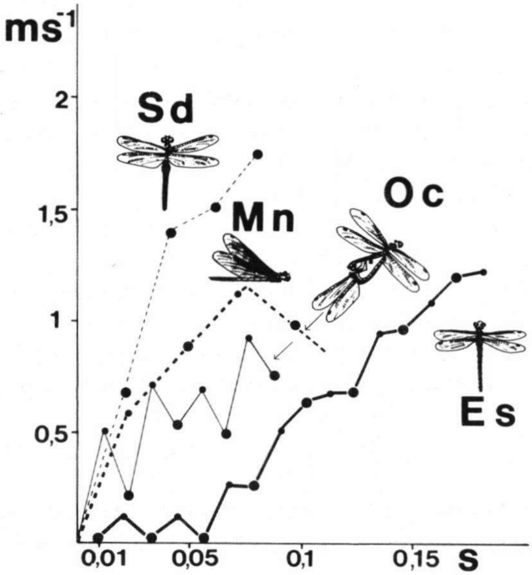

Fig. 6. Comparison of the velocities (ordinate) during the same vertical take-off as in Fig. 5 of individuals representative of various species. Thick dots mark complete stroke cycles, small dots mark the end of each downstroke. Each stroke cycle begins with a downstroke. *Sympetrum depressiusculum* [S.d.], *Mnais navaii* [M.n.], *Orthetrum cancellatum* [O.c.] (in mating position), *Epiophlebia superstes* [E.s.]. M.n. rises only during one and a half wingbeat before decelerating. This species and O.c. beat their wings synchronously here.

come airborne, a further 0.06 s elapsed before it achieved any forward speed; within this period the two anisopterans had reached a flight speed of 1.5 $m.s^{-1}$.

The rates of acceleration during the vertical flight phase, found from the differences in flight speed at consecutive measurements (Fig. 6), also varied widely. *S. depressiusculum* accelerates as rapidly as 35 $m.s^{-2}$, whereas the maximal acceleration found for *E. superstes* was 10,7 $m.s^{-2}$. *M. navaii* also manages distinctly better than *E. superstes*, reaching 23,5 $m.s^{-2}$.

DISCUSSION

Various aspects of flight could be considered on the basis of this analysis: functional morphology, flight technique, the implications for ecology and phylogeny, and physiology. Since insufficient data relative to flight physiology are available, only the first three of these are treated here.

STROKE PATHS AND KINEMATICS OF THE WING JOINTS

Kinematic analysis of the flight of *E. supertes* has revealed some points of agreement with the pertinent morphological evidence on the wing joint. According to PFAU (1986), the structure of the wing joint in Zygoptera and Anisozygoptera is such that the wings beat preferentially in the horizontal plane. This evidence has been confirmed by the slow-motion films of *E. superstes*. The stroke path of Anisoptera is nearly vertical (Fig. 3).

The three suborders can vary the angle of the stroke parth over different ranges. PFAU (1986) found Anisoptera to be most variable in this respect. On the assumption that the values presented here for three anisopteran species are representative of the group, Pfau's finding is confirmed: the range of variation of the angle between stroke path and body long axis was very similar in the Zygoptera and *E. superstes* (37° and 32°, respectively) and considerably larger in the Anisoptera (57°; Fig. 3).

FLIGHT TECHNIQUE

The orientation of the stroke paths in space, here represented by the angle between stroke path and the horizontal, provides evidence as to the manner in which the flight of a given animal is powered. For example, forward flight can be achieved by two different methods. The Calopterygidae and Pseudostigmatidae fly forwards by beating their wings nearly horizontally, holding them pitched up during the backstroke (flight mainly by drag). In contrast during forward beating the angles of attack are much smaller, therefore mainly lift is produced, as the assignment of the stroke phases to the flight paths shows (RÜPPELL, 1985, 1989). The alternative method is to tilt the stroke path forward-down and hold the wings at a small angle of attack in both the down (= forward) stroke and the up (= backward) stroke. Most Anisoptera probably use the second method; as found in the present study, their stroke paths are slanted sharply downward (-83°), especially during forward flight. The stroke-path angles of these species are negative during all manoeuvres except for upward-and-backward flight, implying that they fly mainly by the method with small angles of attack and not by the method mainly with drag.

The Zygoptera exhibit much greater variability in the orientation of their stroke paths to the horizontal while flying in a given direction (RÜPPELL, 1989). During forward flight the stroke path may be steeply inclined (-50°) or nearly horizontal (10°, in this case only shortly performed). Probably they can fly by both methods: with high angles of attack mainly with drag, or with small angles of attack at forwards downwards tilted strokeplane. It is conceivable that they use the latter to fly at a high, constant speed and the drag technique, which requires probably a greater effort, during acceleration. This question needs further study.

For the present, it is impossible to decide whether *E. superstes* uses both methods of propulsion, because its wingbeat frequency is so high that the attack angle of the wings could not be discerned with the method used here. Similarly, it cannot yet be determined how *E. superstes* can fly backwards with a stroke path tilted forward-down at -56°; probably changes in the angle of attack are responsible, but a more detailed analysis would be needed to ascertain this. The responsibility might also lie with nonstationary effects which, according to ELLINGTON (1984a), NACHTIGALL (1980), SAVAGE et al. (1979), SOMPS & LUTTGES (1984) and WEIS-FOGH (1973), appear when an insect is flying with a combination of low flight speed and high stroke velocity.

The angle between the long axis of the body and the flight direction is yet another characteristic of *E. superstes* that places it between the Anisoptera and the Zygoptera. Whereas the slowly flying Zygoptera often fly with their long axis of their body not parallel to the flight direction, the rapid Anisoptera almost always align themselves parallel to the flight direction, a more aerodynamically favourable orientation. *E. superstes* behaves like an anisopteran when flying rapidly and like a zygopteran when flying slowly.

Analysis of the various flying states of *E. superstes* has revealed a flight performance that further corroborates the special position of this relic species. It is characteristic of *E. superstes* that after taking off, which it does with a difficulty rarely observed in dragonflies, it usually proceeds immediately in rapid forward flight. The high flight speed is achieved by relatively high flight muscle mass and a counterstroking wingbeat mode coupled with an extremely high wingbeat frequency. For such flight, stable wings are required. In both the fore- and hindwings some of the veins are unusually thick, especially those in the wing stalk, the anteriormost wing vein (costa) and the pterostigmata.

The consequence of this design, however, is a poor manoeuvrability, so despite of a number of similarities between the wing-joint kinematics of *E. superstes* and the Zygoptera, from which PFAU (1986) deduced that the two should be capable of equally skilful manoeuvres.

Most Anisoptera have a greater body mass and can fly faster than *E. superstes*, but are, nevertheless, considerably more manoeuvrable. The reason is that they can greatly vary the phase relationships of the forewings with respect to the hindwings as well as the direction of the stroke path and the attack angle of the wings. By suddenly changing the stroke path and beating the steeply angled fore- and hindwings in synchrony, Anisoptera can quickly accelerate in a new direction (RÜPPELL, 1989).

Another factor that probably contributes to anisopteran manoeuvrability is the special shape of their wings. Anisopteran wings are broader than those of the Anisozygoptera and can act, therefore, as very effective braking surfaces. The hindwings, in particular, are extremely broad in the proximal region (unlike the stalked wings of Zygoptera and Anisozygoptera); this part of the wing probably serves chiefly as a gliding surface. Furthermore, the braking is performed especially economically with the wing regions close to the body. In this way less force is required to hold a large angle of attack when a broad area, which offers particularly high resistance, is in the proximal rather than the distal part of the wing. By tilting such broad wings more steeply on one side of the body, a flying dragonfly can turn very sharply.

PHYLOGENETIC AND ECOLOGICAL CONSIDERATIONS

The comparison of flight techniques has shown that *E. superstes* occupies a position between the Zygoptera and the Anisoptera; both the mean stroke direction and the angle range of the long body axis with respect to the flight direction are intermediate between those of the two suborders. *E. superstes* is like the Zygoptera in beating the fore- and hindwings in opposite phase, but resembles the Anisoptera with respect to its gliding periods, high wingbeat frequencies and rapid flight. Even in the way it holds its wings while not in flight, *E. superstes* exhibits both zygopteran and anisopteran characteristics; while the insect is hanging at rest, the wings are held together, but shortly before take-off they are spread out horizontally in a posture reminiscent of the Anisoptera. These characters revealed by flight analysis corroborate the phylogenetic position of the Anisozygoptera inferred from morphological characters by ASAHINA (1954), FRASER (1957) and HENNIG (1969) and from functional morphology by PFAU (1986, 1991). According to these authors, the Anisozygoptera and the Anisoptera are descended monophyletically from common ancestors, which very probably flew with the counterstroking wingbeat mode of the Zygoptera.

The results of the flight analysis are also relevant to a discussion of the processes by which the different taxa have become established in their ecological niches. For example, where different species encounter one another, predation may result. The outcome of such interactions depends primarily on the flight techniques employed by the species involved. In comparison between the accelerations and flight speeds achievable by *E. superstes* and the Anisoptera, the flight technique of the former is clearly inferior.

How, then, can *E. superstes* have escaped anisopteran competition and predation pressure and survived for so long? It flies along the mountain brooks in Japan early in the year, when the temperature is low. They fly at air temperatures of about 16°C upwards and even in rainy weather. The Anisoptera appear later in the year. That is, *E. superstes* occupies a temporal niche, where it can succeed because of its energy-conserving flight technique. The counterstroking flight mode (180° out of phase) leads to a very steady forward flight (as described for Zygoptera), which demands no energy-costing accelerations such as occur in calopterygids, pseudostigmatids or in the Anisoptera which beat their wings either phase-shifted or in phase, producing lift or thrust alternately (RÜPPELL, 1989).

The reclusive habit of *E. superstes*, which offers good concealment from predators, also requires none of the high accelerations that can occur, for example, in the vertical take-offs of Zygoptera or Anisoptera (Figs 5-6). *E. superstes* often flies in the shade or, when at rest, hangs hidden within trees or shrubs, with its wings folded against the sides of its abdomen (Fig. 7). When an *E. superstes* hanging in this way is touched, it cannot escape, because it needs a very long warming-up period before it can fly at the low prevailing temperatures. Before take-off *E. superstes* spreads out the wings like the anisopterans and sets them into shivering movement, which is often maintained for more than a quarter of an hour, probably to warm up.

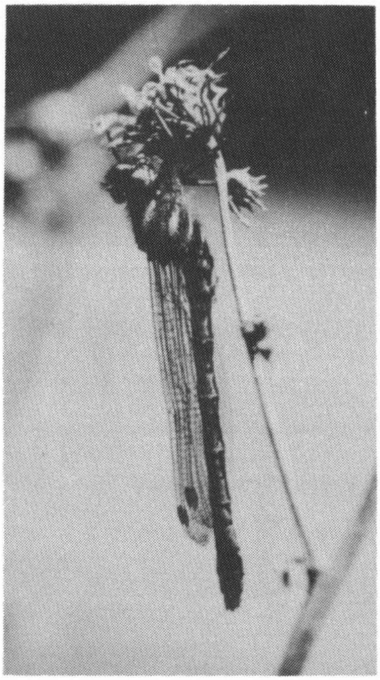

Fig. 7. *E. superstes* male in typical resting posture.

Thermal adaptations in dragonflies have been investigated by MAY (1978). Warming up with the help of buzzing has been examined in Sphingidae (HEINIG, 1990; HEINRICH, 1971). During buzzing the temperature of the thorax of *Manduca sexta* rises strongly (up to 38-42°C) while the temperature of the abdomen approximately reflects the temperature of the surrounding. Besides buzzing, thermoregulation of *E. superstes* is supported by the hairy thorax similar to that of the Sphingidae.

In summary, the flight peculiarities described contribute towards our understanding of the survival strategy of this very inconspicuous, but extraordinarily interesting Mesozoic dragonfly.

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