Odonatologica 17(4): 401-408 *December 1, 1988*

THE ROLE OF THE FULCROALAR MUSCLE IN DRAGONFLY FLIGHT

D.J.S. NEWMAN and R.J. WOOTTON
Department of Biological Sciences, University of Exeter,
Exeter, EX4 4PS, United Kingdom

Received April, 11, 1986 / Revised and Accepted April 18, 1988

Evidence from free-flight cinematography, dissection and manipulation suggests that the fulcroalar muscle in Odonata facilitates wing profile change between Cu and R+M at the start of, and sometimes during, the downstroke by providing some of the power needed to deform the axillary complex. The flexion is completed primarily by the first basalar and second subalar depressors. The fulcroalar muscle may also influence wing deformation at the start of the upstroke. Sectioning shows that it is a single muscle, not two as has been suggested.

INTRODUCTION

The complex, subtle flight of dragonflies is powered and controlled by a mechanism which has many unique features, and has been extensively studied. CLARK (1940), TANNERT (1958), RUSSENBERGER & RUSSENBERGER (1959-60), NEVILLE (1960), HATCH (1966) and PFAU (1986) have all published accounts of the morphology and roles of the flight muscles and, although there is much broad agreement, the differences between these authors' interpretations are a measure of the sophistication of the system. PFAU (1986), whose superb monograph is the most complete account of the odonatan flight apparatus, summarises and tabulates the conclusions of the previous studies. His own reflect an awareness of the importance of fine instantaneous control of the attitude and three-dimensional shape of the wings during the stroke-cycle.

The significance of wing shape-change has been discussed for insects in general by WOOTTON (1981), and is central to a comparative investigation by NEWMAN (1982) of the functional morphology of the wings of a range of dragonfly species. The present paper arises from this work, and offers a new interpretation of the role of the fulcroalar muscle in profile control during the wing-beat.

RIEK & KUKALOVA-PECK (1984) have published a plausible reinterpretation of odonatoid venation, based on new fossil material. For ease of communication we here follow the traditional scheme — but without prejudice.

MATERIAL AND METHODS

Insects studied were *Aeshna cyanea* and *A. grandis, Sympetrum striolatum, Calopteryx splendens* and *C. virgo, Pyrrhosoma nymphula, Enallagma cyathigerum, Ischnura elegans* and *Lestes sponsa.* Despite apparent external differences the structure of thorax and axillae of all these species is essentially similar and the following account probably holds for the Odonata as a whole.

The insects were filmed in free flight, using a Redland Hycam high speed cine camera fitted with a neon timing light. Although the wing beat frequency of Odonata is comparatively low (between 15 and 50 Hz in the insects studied) framing rates of 1000-3000 frames per second were used in order to "freeze" the wings at many points in the stroke-cycle. The film was analysed using a photo-optical data analyser, manufactured by L.W. International, Woodland Hills, California. Among much other information the films revealed details of the nature and timing of the deformations of the wings in flight. The structural origins of these deformations were studied by manipulation and dissection. Fulcroalar muscles of *Aeshna grandis, Calopteryx splendens, Ischnura elegans* and *Enallagma cyathigerum* were embedded, sectioned, and stained in Mallory-Heidenhain for histological examination.

THE WING BASE

The wing base comprises two sclerotised complexes or plates, the humeral complex and the axillary complex (humeral and axillary plates of most authors), partly separated by a band of softer cuticle. Each complex rests on one of the two pleural wing processes, which are situated at the ends of the arms of a Y-shaped structure.

To the humeral complex are attached the leading edge of the wing, and the precostal area if present; and posterodorsally, and movably, the Costa (C). During the wing-stroke the humeral and axillary complexes move relative to each other; this movement and its significance, particularly in the supination process, have been described in detail by NEVILLE (1960).

However, C passes beneath the posterodistal part of the humeral complex and unites firmly with the anterior edge of the axillary complex; and it is also firmly linked with Sc and R+M into an L-girder by the humeral and antenodal cross-veins. All the longitudinal veins hence terminate on the axillary complex; and it follows that any actively-induced deformations of the wing which involve relative movements of these veins must stem from distortions of the axillary complex itself.

A diagrammatic posteroventral view of the underside of the humeral and axillary complexes, associated vein bases and principal depressor muscles of an anisopteran is shown in Figure 1, with the pleuroaxillary membrane removed.

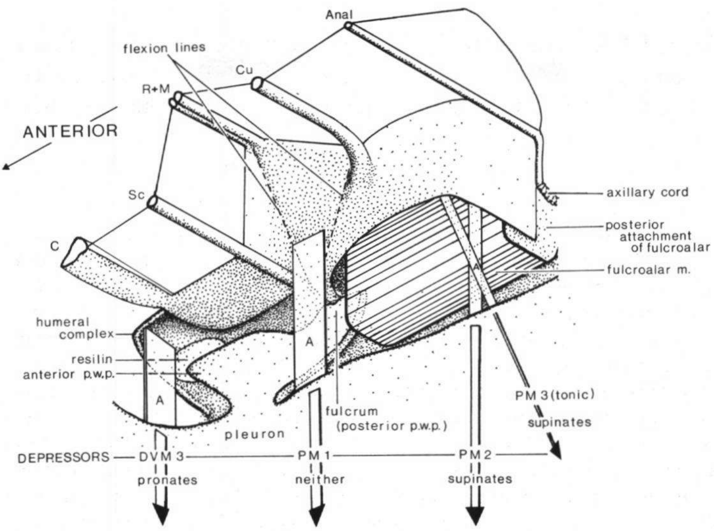


Fig. 1. Diagrammatic posteroventral view of left forewing base of an anisopteran dragonfly. The pleuroaxillary membrane is removed. The axillary complex and attached wing area fill the upper foreground; the humeral complex is visible behind to the left. — [A: apodeme; — C, Cu, R+M, Sc: wing veins; — DVM3: first basalar muscle; — m: muscle; — PM1, PM2, PM3: first second and third subalar muscles; — p.w.p.: pleural wing process].

Figure 2 shows diagrammatically a series of posterodorsal views of the axillary complex alone.

The axillary complex can be regarded as a sprung box, open ventrally, whose side walls can be deformed by the action of the flight muscles. R+M, with Sc lying vertically beneath, form the front wall of the box. The other veins run into the outer side wall. The principal deformation of the wing base which the complex allows is the movement of the base of the cubitus (Cu) relative to those of R+M and Sc. This is made possible by the bending of a section of the outside wall, between R+M and Cu, which has two approximately vertical flexion-lines (Figs 1, 2). Of these, the posterior line is the less flexible. The flexion-lines allow this section — usually interpreted as part of the subalar sclerite — partly to rotate around a vertical axis. This makes the side wall effectively shorter, and brings the bases of the two veins R+M and Cu closer together (Fig. 2).

This section of the side wall of the complex extends ventrally, turning inwards under the box, becoming horizontal, and articulating with the posterior pleural wing process. It is suggested that the fulcroalar muscle plays an important part in the deformation of the axillary plate.

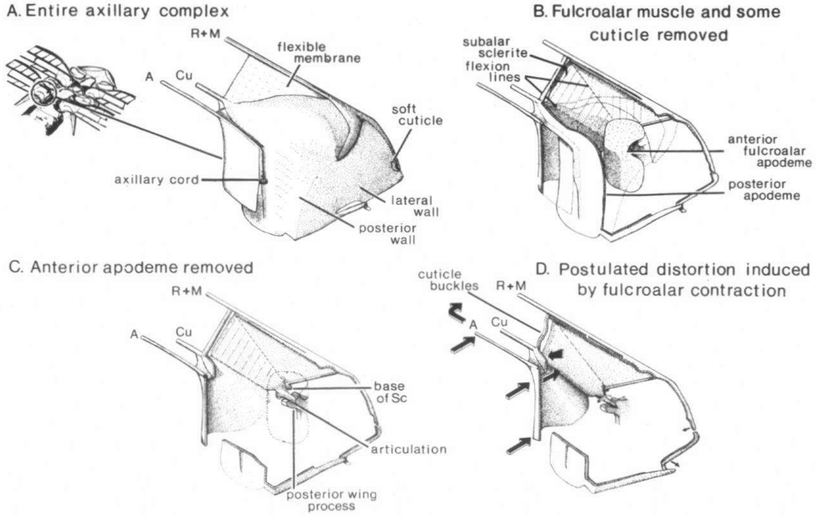


Fig. 2. Diagrammatic posterodorsal view of left axillary complex of an anisopteran, showing postulated effect of fulcroalar muscle. The combined effects of the contractions of the fulcroalar and wing depressor muscles pull the posterior wall of the axillary complex forward and the subalar sclerite down, thereby moving the base of Cu out, forward and down. — [A, Cu, R+M, Sc: wing veins].

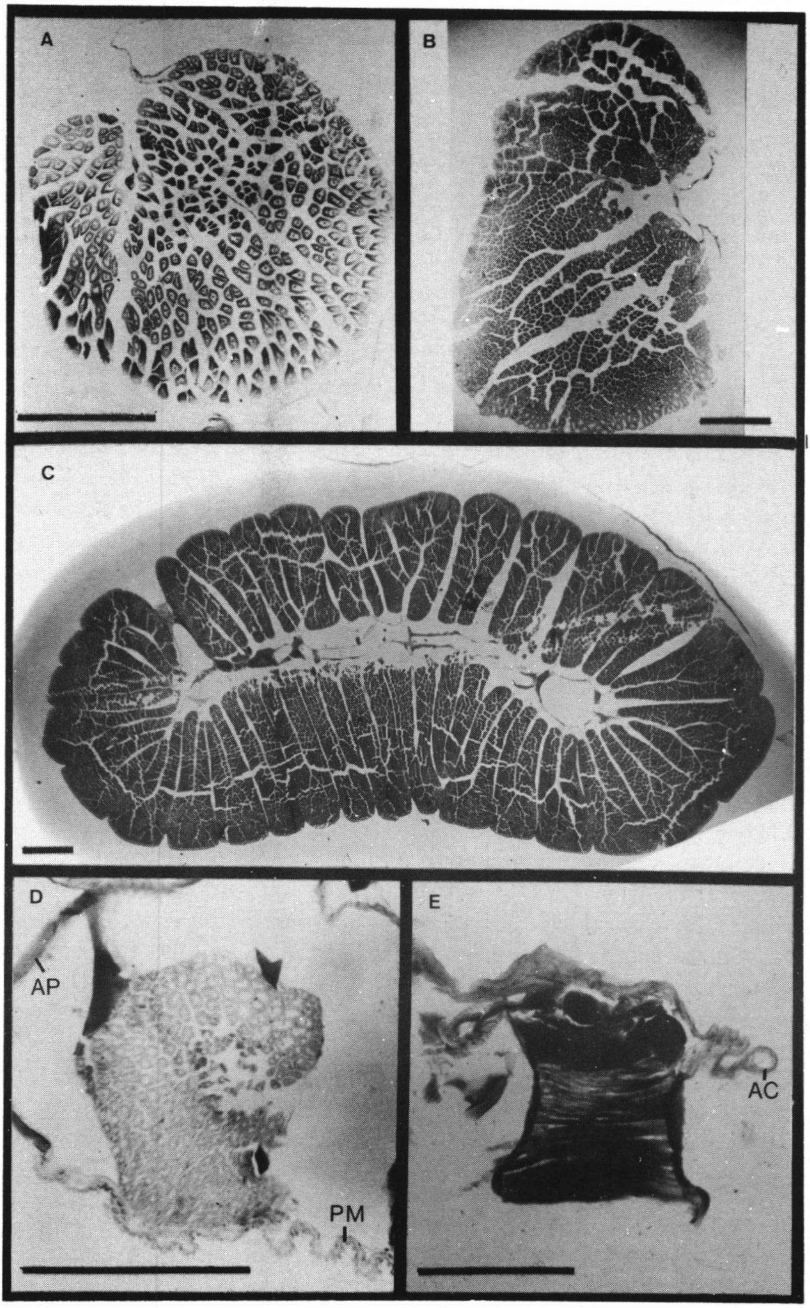
THE FULCROALAR MUSCLE

The fulcroalar muscle (PM4 of CLARK, 1940 and HATCH, 1966) is a small muscle within the axillary complex, running from its posterior wall to a kidney-shaped apodeme inserted on the posterior pleural wing process. Since the posterior end is firmly attached to the complex the whole muscle will swing, and rotate around its longitudinal axis, as the wing beats. The anterior apodeme has a flexible tendon linking it to the pleural wing process, which presumably allows the whole muscle to oscillate, so avoiding damage.

It is disputed in the literature whether this muscle is single or double. CLARK (1940), TANNERT (1958) and HATCH (1966, quoting Tannert) state that it is double. NEVILLE (1960) and TILLYARD (1913) maintain that it is single.

CLARK (1940) places the "two" muscles, PM4 a and b, diagonally side by side. TANNERT (1958) describes them as being one above the other. Tannert states

Fig. 3. Cross-sections of fulcroalar muscles: (A) *Calopteryx splendens;* — (B) *Aeshna grandis;* — (D) *Ischnura elegans.* — (C) Cross-section of first subalar muscle of *Aeshna grandis* for comparison. (E) Longitudinal section of fulcroalar muscle of *Enallagma cyathigerum.* — [AC: axillary cord; — AP: part of axillary complex; — PM: pleural membrane. — Each scale bar represents 200 μm].


A
B
C
D
AP
PM
E
AC

that the two muscles act antagonistically, raising and lowering a trailing edge flap.

This is improbable on functional grounds. If two muscles were present they could not be antagonistic because:

(1) The single anterior kidney-shaped apodeme can pivot on its flexible tendon. This would nullify the contraction of a muscle occupying half the apodeme.

(2) The posterior attachment on the back wall of the axillary complex does not, as TANNERT (1958) states, pivot around a line that continues the line of the anal vein across the posterior wall.

SIMMONS (1977), studying the nervous systems of *Hemianax papuensis* and *Aeshna brevistyla*, both Anisoptera, indicates that the nerve supply to "PM4 a+b" is double, the nerve bifurcating before entering the muscle(s). However, this need not indicate a double muscle, as a similar situation is indicated for DVM3, the first basalar, which is certainly a single muscle.

Histological investigations show no evidence that two muscles are present. PM4 muscles of *Aeshna grandis* and whole wing-bases of *Calopteryx splendens*, and *Ischnura elegans* were sectioned and the transverse sections of the fulcroalars compared with similarly treated phasic flight muscles (Fig. 3). Since the muscle appears to be undivided, and we cannot envisage how such a pair of muscles could act antagonistically, we conclude that PM4 is single.

THE FUNCTION OF THE FULCROALAR MUSCLE

Figure 1 illustrates diagrammatically the sites of action of the principal wing depressor muscles. These are the first basalar muscle (DVM3 of CLARK, 1940 and HATCH, 1966), whose apodeme is inserted on the humeral complex, anteriorly to the pleural wing processes; the first subalar muscle (PM1 of Clark and Hatch); and the second subalar muscle (PM2 of Clark and Hatch). Power--producing muscles may also play a part in wing attitude control; and it is generally agreed that DVM3 tends to pronate the wing, that PM2 tends to supinate it, and that PM1, being directly opposite the posterior pleural wing process, does neither. The smaller, tonically contracting third subalar muscle (PM3) and the little second basalar (DVM4 of Clark and Hatch, and not shown in Fig. 1) would tend, respectively, to supinate and to pronate the wing, but would generate comparatively little force.

When the functioning of the axillary plate is considered, certain anomalies are evident. For some parts of the wing stroke the wing shows little deformation, which implies that the axillary complex must be rigid enough to resist deformation by the power-producing muscles. This is true during the middle part of the downstroke, where DVM3 and PM3 are tending respectively to pronate and to supinate the wing, and hence to bend the axillary complex over the pleural wing process. Were the complex not rigid, the wing would develop an inappropriate degree of camber by flexion between R+M and Cu.

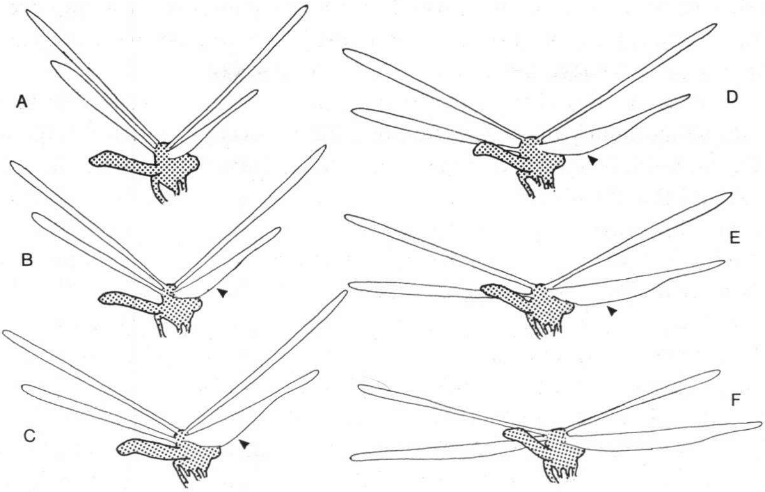


Fig. 4. Tracings from a high-speed cine film of *Calopteryx virgo*, showing the lowering of a posterior flap (arrowed) on the right hind wing during a left turn. The traced frames are from a single wing-beat cycle and are 12.5 ms apart.

At other times, however, flexion does occur between these veins: apparently as the wing is pronated at the start of the downstroke, and probably in the generation of the complex twisted shape which accompanies supination at the beginning of the upstroke. It also occurred when a trailing edge flap was seen to be lowered in one wing in a film of *Calopteryx virgo* (Fig. 4).

It seems, therefore, that the flexion-lines in the axillary complex must be rigid enough to withstand the combined action of PM2 and DVM3 alone — even though these act at opposite ends of the complex, and hence seem perfectly placed to cause the distortion of the side wall shown in Figure 2 — and that additional effort is needed to deform the complex.

The fulcroalar muscle also seems ideally situated to bring about this deformation. However, electrical stimulation in vivo of the fulcroalar muscles of *Aeshna cyanea* produced a contraction, but no apparent change in the shape of the wing or the axillary complex.

It seems possible that the fulcroalar muscle provides only a proportion of the power necessary to deform the complex. When the fulcroalar is contracted the flexion lines in the side wall are effectively weakened, so that the plate can be deformed by the action of the main flight muscles (Fig. 2). This is an elegant solution, since a fulcroalar capable by itself of flexing the wing base would probably need to be impracticably large.

REFERENCES

CLARK, H.W., 1940. The adult musculature of the anisopterous dragonfly thorax (Odonata, Anisoptera). *J. Morph.* 67: 523-565.

HATCH, G., 1966. Structure and mechanics of the dragonfly pterothorax. *Ann. ent. Soc. Amer.* 59(4): 702-714.

NEVILLE, A.C., 1960. Aspects of the flight mechanics of anisopterous dragonflies. *J. exp. Biol.* 37: 631-656.

NEWMAN, D.J.S., 1982. *The functional wing morphology of some Odonata.* Ph. D. thesis, Univ. Exeter, Exeter, England.

PFAU, H.K., 1986. Untersuchungen zur Konstruktion, Funktion und Evolution des Flugapparates der Libellen. *Tijdschr. Ent.* 129: 35-123.

RIEK, E.F. & J. KUKALOVÁ-PECK, 1984. A new interpretation of dragonfly wing venation based on Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in insect wings. *Can. J. Zool.* 62(6): 1150-1166.

RUSSENBERGER, H. & M. RUSSENBERGER, 1959-60. Bau und Wirkungsweise des Flugapparates von Libellen. *Mitt. naturf. Ges. Schaffhausen* 27: 1-88.

SIMMONS, P., 1977. The neuronal control of dragonfly flight. I. Anatomy. *J. exp. Biol.* 71: 123-140.

TANNERT, W., 1958. Die Flügelgelenkung bei Odonaten. *Dt. ent. Z.* (N.F.) 5: 394-455.

TILLYARD, R.J., 1917. *The biology of dragonflies.* Cambridge Univ. Press, Cambridge.

WOOTTON, R.J., 1981. Support and deformability in insect wings. *J. Zool. Lond.* 193: 447-468.