A NEW AESHNID DRAGONFLY FROM THE LOWER CRETACEOUS OF SOUTH-EAST ENGLAND

by E. A. JARZEMBOWSKI

ABSTRACT. A comparatively advanced 'hawker' dragonfly (*Valdaeshna surreyensis* gen. et. sp. nov., Aeshnidae: Gomphaeschninae) is described from the late Hauterivian of the Weald. The single male specimen shows body 'colour' markings as well as full venational details of the fore and hindwings and is the most complete early aeshnid found to date. Fossil preservation, association, and palaeoenvironment are briefly discussed.

THE most intact example of an early aeshnid dragonfly was found by the author in April 1986 in the Wealden Series of south Surrey whilst on field-work with the West Sussex Geological Society and is described below. It has been popularly dubbed the Surrey Dragonfly (Jarzembowski 1987*a*) and is formally named here *Valdaeshna surreyensis* gen. et sp. nov.

The earliest record of a true dragonfly (Odonata: Anisoptera) is from the Upper Lias (late Lower Jurassic), but doubts have been expressed recently as to whether any extant families of dragonflies occurred as early as the Mesozoic (Hennig 1981). A Palaeocene origin of the family Aeshnidae, the living 'hawker' dragonflies of north-west Europe, has been suggested (Carle 1982). However, subsequent finds of isolated wings in Europe and Asia suggested that Aeshnidae had appeared by the Lower Cretaceous (Hong 1982; Jarzembowski 1984). The new find shows body details as well as a complete venation and provides evidence that comparatively specialized Aeshnidae existed by the early Cretaceous.

Locality and horizon. The specimen is preserved in a phosphatic concretion from the disused pit of the former Auclaye Brickworks, Surrey (national grid reference TQ 170 388). This pit was worked in the Lower Weald Clay above the Okehurst Sand (Worssam 1978).

Associated Fauna. Other insects found in concretions from the same locality include beetles (Coleoptera), bugs (Hemiptera), crickets (Orthoptera), wasps (Hymenoptera), true flies (Diptera), caddis flies (Trichoptera), scorpion flies (Mecoptera), and lacewings (Neuroptera) (Jarzembowski 1987*b*). The insects occur with clam shrimps (Crustacea: Conchostraca), sea slaters (Crustacea: Isopoda), fish scales, coprolites, and comminuted plant debris, the latter often fusainized.

Palaeoecology. The insects are represented mainly by dissociated skeletal elements of adults (imagines), including detached wings and body parts and plates (sclerites). Intact specimens are rare. The conchostracan *Cyzicus subquadratus* (J. de C. Sowerby) is locally abundant; the valves are commonly paired and unworn. Isopoda are represented by undescribed bodies of sea slaters which are incomplete but not dissociated like the insects.

The isopods suggest a salt-water depositional palaeoenvironment which is consistent with the absence of immature freshwater insects such as aeshnid larvae. The adult insects could have been blown or washed in; intact Coleoptera (Carabidae?) and Hemiptera (Homoptera) have their wings folded suggesting the latter. The insect remains are poorly sorted and any fluvial influence was probably weak. *C. subquadratus* commonly occurs with freshwater Mollusca in the late Jurassic–early Cretaceous of southern England (Morter 1984) but there is no such association at the Auclaye Brickworks. Some extant species of *Cyzicus* occur in both fresh and brackish water (Tasch 1969).

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Salinity tolerance is suggested in some Mesozoic species because *Cyzicus* (= *Estheria*) *murchisoniae* (Jones) from the Middle Jurassic of Scotland occurs in both fresh and brackish water assemblages in shallow lagoonal deposits (Hudson 1963*a*, *b*). The pit faces at the Auclaye Brickworks are too degraded for detailed palaeoecological work but the fossil arthropods from concretions provide environmental pointers consistent with lagoon-bay models for the Weald Clay (Allen 1981).

Preservation. The dragonfly is not on a single bedding plane, the various parts occupying a 10 mm thickness of sedimentary rock. The thorax and wing folds are preserved in relief although the former is slightly compressed. The right forewing, which is preserved at an angle of 25° to the plane of the body and the other three wings, is also slightly compressed. The abdomen is bent (text-fig. 3A). The pterostigma (text-fig. 2, p) and veins are brown-tinted but membraneous areas of the wings are the colour of the matrix. The body is distinctly patterned (text-fig. 3A) with brown markings.

Alongside the dragonfly is a forewing of a mesoblattinid cockroach. The only other fossils in the same parting are sinuous burrows on the hindwings of the dragonfly. They are mainly on the upper side of the membrane and veins may be depressed along their courses. Some of the worm (nematode?) traces are very small (text-fig. 3B).

Taphonomy. The dragonfly was evidently buried rapidly and there was some compaction of sediment prior to cementation. The burrows were clearly formed when sediment and wings were soft and pliable, but the lack of traces around the body suggests that they were not produced by exiting parasites.

Dragonfly wings are permanently outstretched in life at right angles to the body and the abdomen is a flexible cylinder. In the fossil the right forewing and abdomen are bent suggesting that soft cuticle had started to decay prior to burial. I have observed that dead dragonflies floating in a laboratory fish tank readily develop breaks in the abdomen. The thorax is lying on its left side and the posterior part of the abdomen is bent to the right which suggest that the dragonfly floated with its dorsal side uppermost.

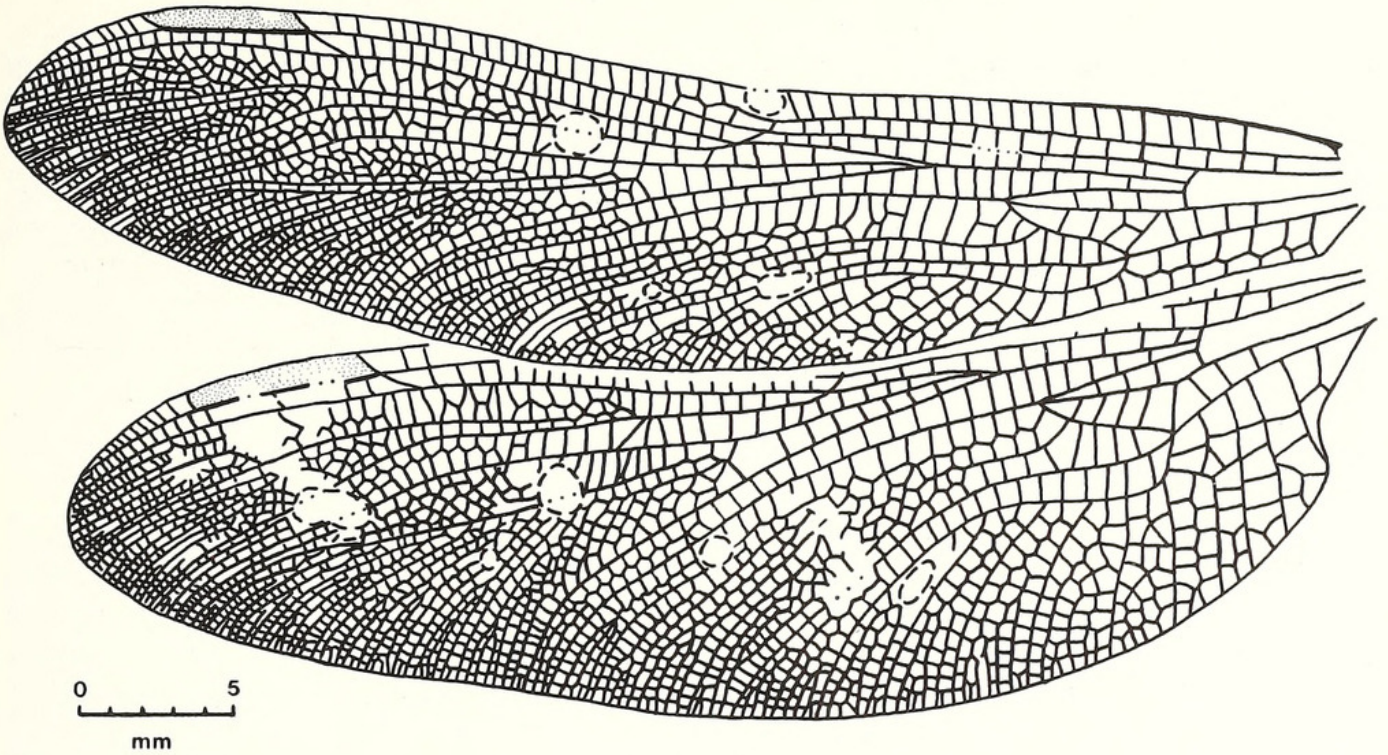
'Colour' pattern is commonly preserved in Wealden fossil insects. The pattern is due to the survival of heavily tanned (sclerotized) and darkly pigmented areas. The black or brown coloration in Wealden insects resembles that of Recent relatives although no traces of non-melanic pigments have yet been observed (Jarzembowski 1984). The brown coloration of the veins and pterostigma of *V. surreyensis* is similar to that of many Recent dragonflies. The wing membrane is commonly clear (hyaline) in Recent Odonata and could have been originally so in *V. surreyensis*. The bodies of living aeshnids are usually brown, spotted with blue or green, sometimes with yellow stripes or spots on the sides of the thorax (Walker 1958). Only the brown body patterning has survived in *V. surreyensis* delimiting non-melanic areas.

SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758
Order ODONATA Fabricius, 1792
Suborder ANISOPTERA Selys, 1840
Superfamily AESHNOIDEA Leach, 1815
Family AESHNIDAE Leach, 1815
Subfamily GOMPHAESCHNINAE *sensu* Lieftinck, 1968
Genus VALDAESHNA gen. nov.

Diagnosis. Gomphaeschnine with one row of cells separating the anterior median vein (MA) from the median supplementary vein (Mspl) in the hindwing, supplementary anal loop absent, subcostal vein (Sc) continuing beyond the nodus (N), and an incomplete basal antenodal (Ax) in fore and hindwings.

Type species. *Valdaeshna surreyensis* sp. nov.



TEXT-FIG. 1. *Valdaeshna surreyensis* gen. et sp. nov. In. 64632. Left forewing and hindwing showing venation.

Valdaeshna surreyensis sp. nov.

Text-figs. 1–3A, 4A, B

Derivation of name. Named after the Weald, County of Surrey and extant odonatan genus *Aeshna*.

Diagnosis. As for genus.

Holotype. In. 64632*a*, *b*, British Museum (Natural History).

Locality. Auclaye Brickworks pit, near Capel, Surrey, England (national grid reference TQ 170 388).

Horizon. Lower Weald Clay, clay interval above British Geological Survey sandstone 3a (Gallois *et al.* 1972); early Cretaceous: (?)late Hauterivian (Worssam 1978).

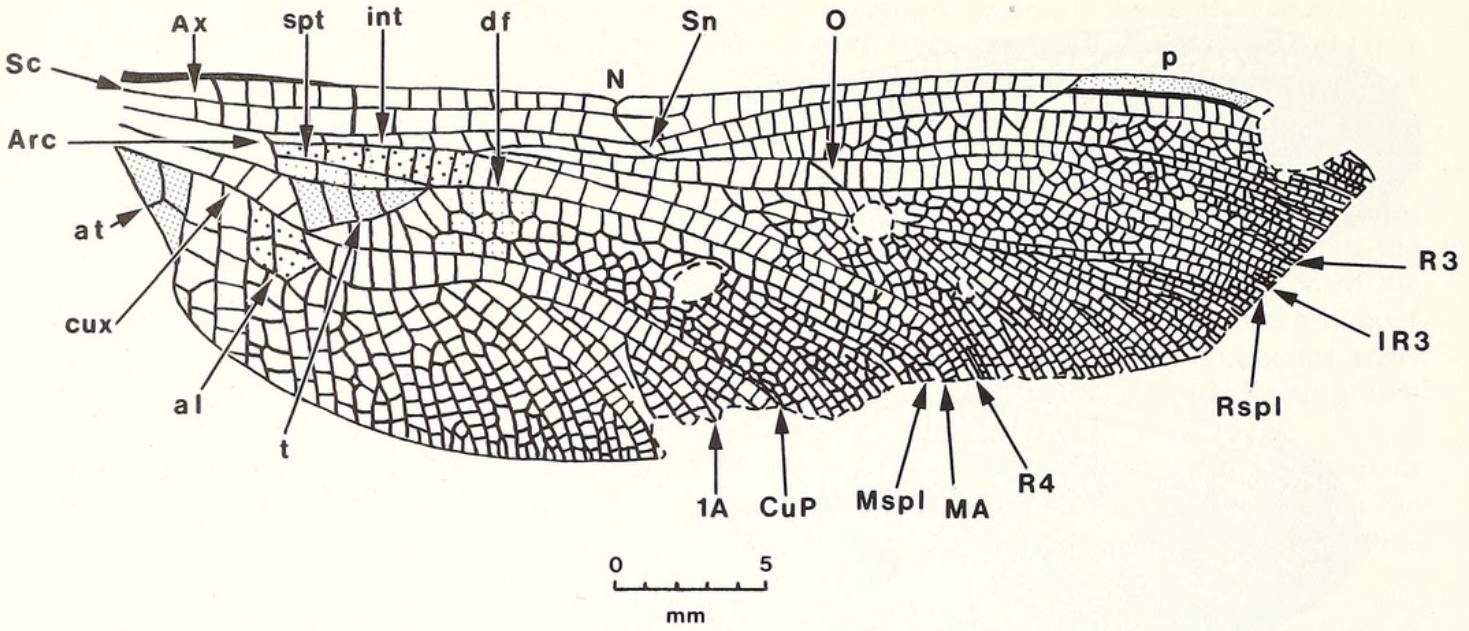
Description. The holotype is described as exposed naturally in a frost-cracked phosphatic concretion. For abbreviations see text-fig. 2.

The thorax (text-fig. 3A) is exposed posteriorly from the mesothoracic spiracle (s) immediately above the mesokatepisternum. The dorsal carina (dc) and pre-alar ridge (pr) are prominent. Brown markings are preserved on the pterothorax (synthorax auctt.) The mesepisternum (humeral region auctt.) shows two stripes one of which, the mid-dorsal, is truncated anteriorly. The humeral stripe is present overlying the mesopleural suture (ms) and is partly divided by the latter. The interpleural and metapleural stripes lie immediately behind their respective sutures.

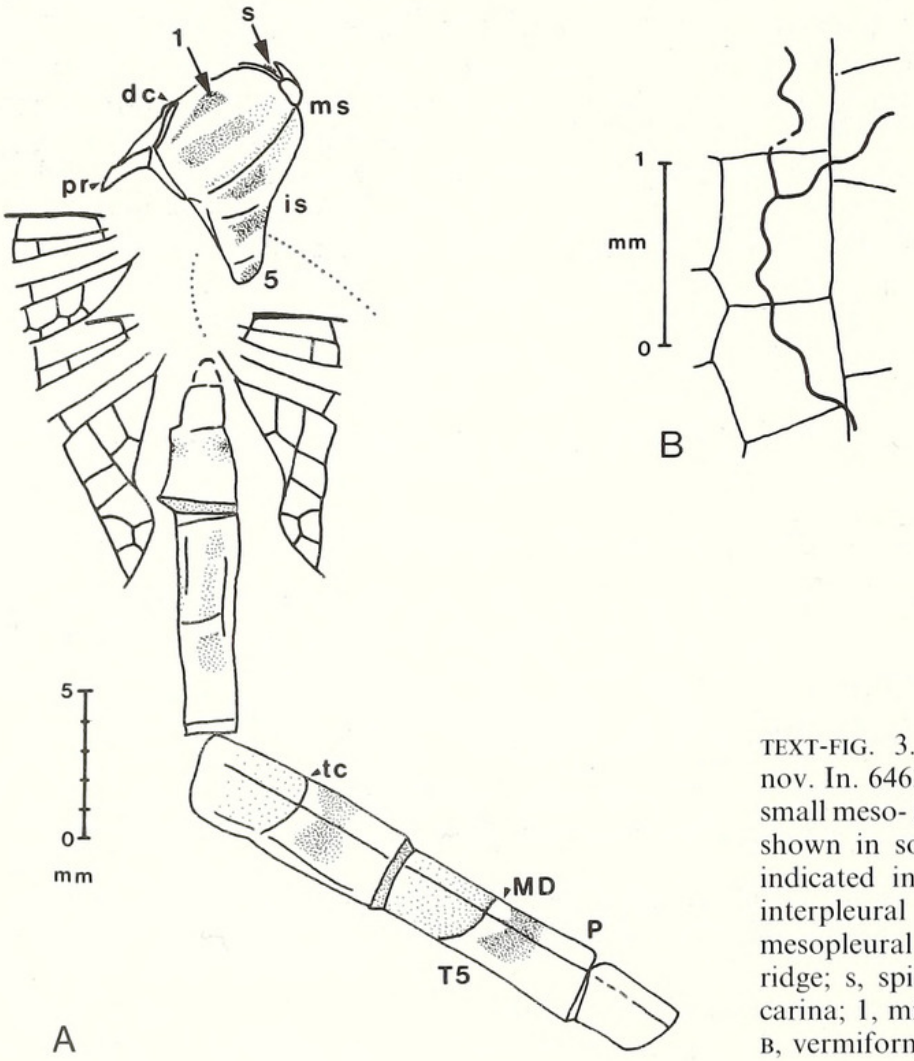
The wings are hyaline, veins dark brown, pterostigma (p) pale brown. The anal triangle (text-fig. 2, at) is developed as in Recent male Anisoptera. An incomplete basal antenodal (Ax) is present. The subcostal vein (Sc) continues beyond the nodus (N).

Other venational characters in the Surrey Dragonfly are as follows, the numbers referring to characters used in a recent phylogenetic study of gomphaeschnine dragonflies by Wighton and Wilson (1986) and discussed below.

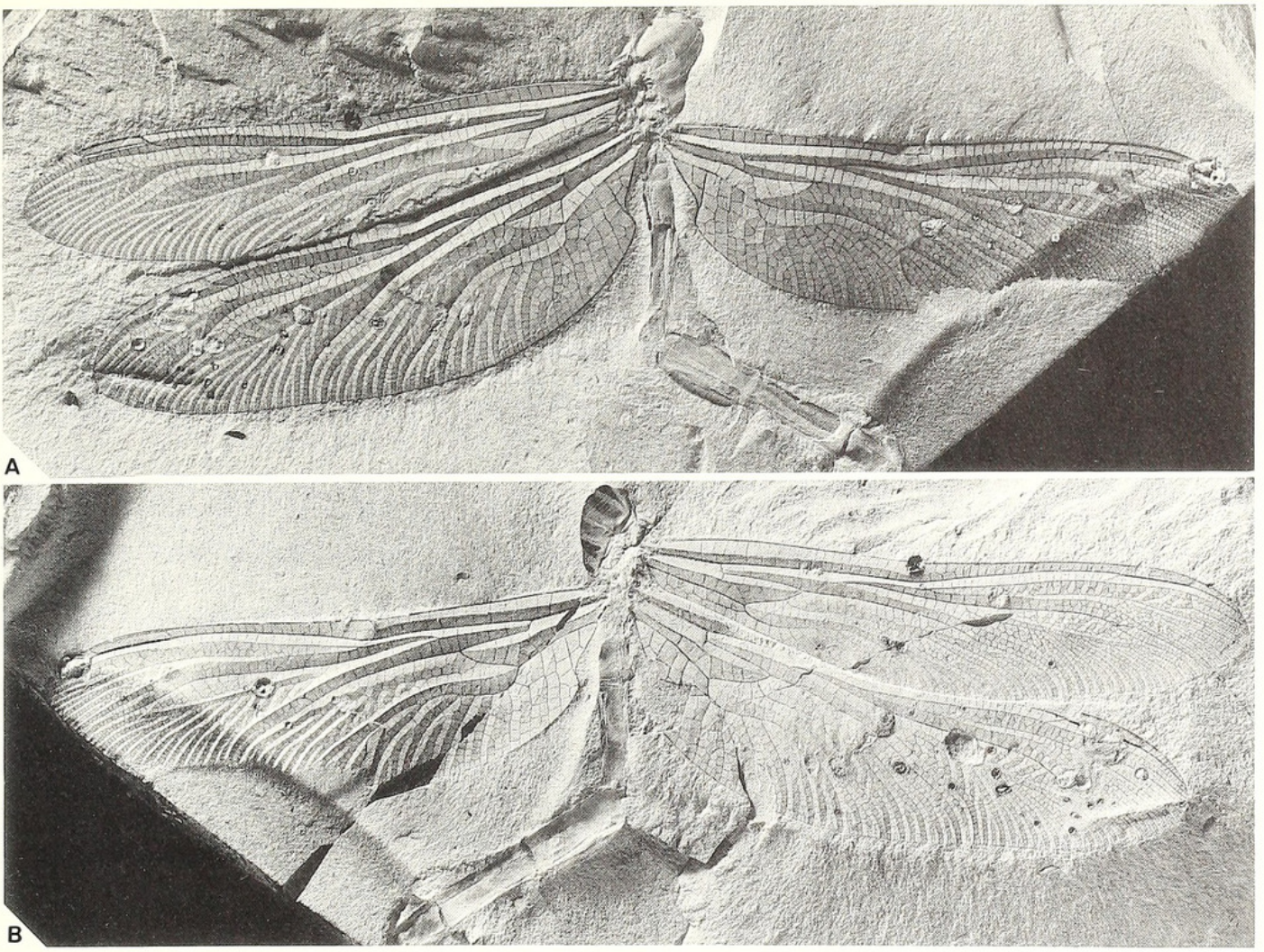
1 hind and forewing triangles (t) are approximately equal in length;
2 all triangles are relatively narrow;



TEXT-FIG. 2. *Valdaeshna surreyensis* gen. et sp. nov. In. 64632. Right hindwing with explanation of venation. al, anal loop; Arc, arculus; at, anal triangle; Ax, antenodal; CuP, posterior cubitus; cux, cubito-anal crossvein; df, discoidal field; int, middle fork; IR3, third intercalary; MA, anterior median; Mspl, median supplementary; N, nodus; O, oblique; p, pterostigma; R3, third radial; R4, fourth radial; Rspl, radial supplementary; Sc, subcostal; Sn, subnodus; spt, supratriangle; t, triangle; 1A, anal.



TEXT-FIG. 3. *Valdaeshna surreyensis* gen. et sp. nov. In. 64632. A, dorsal aspect of body excluding small meso- and metathoracic sclerites. Wing bases shown in solid lines, position of right forewing indicated in dotted lines. dc, dorsal carina; is, interpleural suture; MD, mid-dorsal spot; ms, mesopleural suture; P, posterior spot; pr, pre-alar ridge; s, spiracle; T5, fifth tergite; tc, transverse carina; 1, mid-dorsal stripe; 5, metapleural stripe. B, vermiform casts in anal area of left hindwing.



TEXT-FIG. 4. *Valdaeshna surreyensis* gen. et sp. nov. holotype. A, dorsal view, In. 64632*a*. B, ventral view, In. 64632*b*. ×1·6.

3 the anal loop (al) has few (four or five) cells;
4 a supplementary anal loop is absent;
5 a median supplementary vein (Mspl) is present;
6 the radial supplementary vein (Rspl) is well developed;
7 the basal discoidal field (df) in the hindwing has three rows of cells;
8 the posterior cubitus (CuP) and anal vein (1A) in the hindwing are separated by several rows of cells distally;
9 there is more than one cubito-anal crossvein (cux);
10 the oblique vein (o) is far from the subnodus (Sn);
11 the fourth radial (R4) and anterior median (MA) veins are parallel distally;
12 three crossveins are present in the hindwing supratriangle (spt);
13 seven intermedian crossveins are present in the area basad of the middle fork (int) in the hindwing;
14 MA is separated from Mspl by a single row of cells in the hindwing;
15 the third intercalary vein (IR3) is simple.

The abdomen is preserved up to segment 6, the last segment being weathered and truncated at the edge of the concretion. Typical (elongate) segments possess transverse and dorsal carinae (tc, dc) and show colour pattern. The mid-dorsal spots (MD) are united to form a light band which tapers away from the dorsal carina, i.e. MD is 'triangular'. The tergum immediately behind MD is dark. The posterior spots (P) are united to form a light area larger than MD.

DISCUSSION

The presence of triangles (t) and supratriangles (spt) in the fore and hindwings identifies *V. surreyensis* gen. et sp. nov. as an anisopteran or dragonfly in the strict sense (Hennig 1981). As in Recent Anisoptera, the presence of an anal triangle (at) in the hindwing shows that the type is a male. The triangles are similar in shape, possess crossveins, and are equidistant from the arculus (Arc) in *V. surreyensis* as in the superfamily Aeshnoidea and family Aeshnidae (Davies and Tobin 1985).

V. surreyensis is placed in the extant subfamily Gomphaeschninae on a combination of venational characters: the third intercalary vein (IR3) is simple and not forked as in other subfamilies Aeshninae (Fraser 1957, fig. 50) and Brachytroninae (F. Nanninga in O'Farrell 1970, fig. 13.4); an anal loop (al) is present; the third radial vein (R3) has an anterior convex curve behind the pterostigma (p); the fourth radial (R4) and anterior median (MA) veins are parallel; and the radial supplementary (Rspl) and median supplementary (Mspl) veins are well developed, unlike in Neopetaliinae (Wighton and Wilson 1986). The only other evidence of Gomphaeschninae in north-west Europe is from the Bembridge Marls (late Eocene/early Oligocene) of the Isle of Wight (Cockerell and Andrews 1916).

V. surreyensis has some unusual venational characters useful for identification. Sc extending beyond the nodus (N) and the presence of an incomplete basal antenodal (Ax) in the fore and hindwings are unusual characters in Anisoptera and the combination of these characters in *V. surreyensis* appears to be unique. Sc extends beyond N in some extant Aeshninae (*Neuraeschna* and *Staurophlebia*: Professor D. A. L. Davies, Mr S. J. Brooks, pers. comms.) and an incomplete basal Ax may occur in Brachytroninae (*Periaeschna*: Fraser 1936, fig. 23). Species of *Cephalaeschna* (= *Indophlebia*, Brachytroninae) may have an incomplete basal Ax in the hindwing (Fraser 1936, fig. 17) or Sc continuing beyond N in the forewing (Fraser 1936, fig. 26) but not in combination as in *Valdaeshna*.

The 'colour' pattern of *V. surreyensis* shows some aeshnid and gomphid features. The mid-dorsal spots (MD) resemble *Boyeria* (Walker 1958, pl. 17, figs. 1 and 2) but the thoracic colour pattern resembles extant *Gomphus* (family Gomphidae: Walker 1958, pl. 40) except that the mid-dorsal stripe is well separated from the dorsal carina and the interpleural and metapleural stripes are slightly more posterior in *Valdaeshna*. An incomplete basal Ax may also be developed in the forewing of *Gomphus* (Fraser 1934, fig. 63). However, gomphid-like characters in late Mesozoic Anisoptera are probably symplesiomorphies (Hennig 1981) and therefore do not affect the systematic placing of *Valdaeshna*.

In the above description, I have numbered 1–15 characters used in a recent phylogenetic study of gomphaeschnine genera (Wighton and Wilson 1986). If the characters are scored 0 = primitive and 1 = advanced, then the character states for *Valdaeshna* are:

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
0	1	0	0	1	1	1	1	1	0	1	1	1	0	0

Valdaeshna shares the largest number of advanced characters (seven) with extant *Boyeria* and Tertiary *Oplonaeschna* in the subfamily Gomphaeschninae, but also shares nine advanced characters with genera of Aeshninae and Brachytroninae. Wighton and Wilson considered that *Boyeria* was one of the most advanced genera of Gomphaeschninae and most closely related to Brachytroninae/Aeshninae, although its similarity to the gomphaeschnine *Oplonaeschna* was interpreted as parallel or convergent evolution in the latter genus. Gomphaeschninae are clearly not a holophyletic (monophyletic) group, but *Valdaeshna*, like *Boyeria* and *Oplonaeschna*, may be considered a comparatively specialised aeshnid.

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