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# THE AFFINITIES OF *AESHNA BREVISTYLA* (RAMBUR) (ANISOPTERA: AESHNIDAE)

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The Australasian dragonfly *A. brevistyla* is compared with its congeners, all geographically distant, and with spp. in other aeshnine and allied anactine genera. The results of these comparisons emphasise its taxonomic isolation, in particular from the South American spp. of *Aeshna* to which it had been thought to be allied. It appears to be more closely allied to the specialised Papuan and New Caledonian genus *Oreaeschna*, of which it may represent a forerunner. A new, monotypic subgenus of *Aeshna*, *Adversaeschna*, is described to receive it.

## INTRODUCTION

RAMBUR (1842) described *Aeshna brevistyla* (as a species of *Aeschna* Anon.) from Australia, and its placement in that genus has, to my knowledge, been accepted since. However, *A. brevistyla*'s range, through Australia, except for much of the tropics, to New Zealand and the adjacent south-west Pacific (cf. WATSON, 1981; DAVIES & TOBIN, 1985) is remote from those of other species of *Aeshna* Fabricius, which together extend across the Palaearctic and Nearctic regions, down into southern Africa and South America (PINHEY, 1952; CALVERT, 1956) and to India and China (DAVIES & TOBIN, 1985)*.

FRASER (1957) compared *A. brevistyla* and two South American species, *A. bonariensis* (Rambur) and *A. confusa* (Rambur), and concluded that "there no longer remains any doubt about their near relationship and so, the probable

* LICHTENSTEIN (1796) described *Aeshna javana*, presumably from Java, but the text (p. 189) suggests a species of *Anax* ("Aeshna thorace concolore fusco, abdomine juxta spiracula maculis flavis"). It is, however, difficult to place his *Aeshna flavifrons* from south-east India ("Aeshna thorace striato fronte labiisque exalbidis. Habitat in Coromandel. Adfinis A. Javanae, sed multo minor.") (p. 189).

derivation of *brevistyla* from ... South America" (p. 99) (see also WATSON, 1981). On the other hand CALVERT (1956 and earlier papers) placed these two South American *Aeshna* in different subgenera: *bonariensis* in *Neureclipa* Navas (its type species) and *confusa* in *Hesperaeschna* Cockerell. The question then arises: where does this leave *A. brevistyla*?

VICK & DAVIES (1990) provided an intriguing part-answer by suggesting that their new species *Oreaeschna dominatrix* from New Caledonia is annectant between the New Caledonian form of *Aeshna brevistyla* and the New Guinean *Oreaeschna dictatrix* Lieftinck.

Recent access to extensive collections of Old- and New World species of *Aeshna* and allied genera has given me the opportunity to address this question. The results form the subject of this paper.

## MATERIAL EXAMINED

Much of the material examined is lodged in the Florida State Collection of Arthropods, Gainesville, FL, U.S.A., or in the collection of the International Odonata Research Institute, also in Gainesville. Specimens in the Australian National Insect Collection, Canberra, Australia, and the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands, were also examined. A few species were documented from the literature.

The species checked, arranged in alphabetical order by genus/subgenus, were as follows. Type species are marked with an asterisk. Although *Aeschna* is junior synonym of *Aeshna* (cf. HOUSTON & WATSON, 1988), no distinction is drawn in this list between citation of authorship of species-group names originally allocated to one or other of the two genera.

*AESHNA (AESHNA)* FABRICIUS
*affinis* Vander Linden
*arida* Kennedy (from NEEDHAM & WESTFALL, 1955)
*brevistyla* Rambur
*clepsydra* Say
*caerulea* Ström
*constricta* Say
*crenata* Hagen
*cyanea* (Müller)
*eremita* Scudder
**grandis* (Linnaeus)
*interrupta* Walker (incl. ssp. *interna* Walker and *lineata* Walker)
*juncea* (Linnaeus) (incl. ssp. *americana* Bartenef)
*minuscula* McLachlan
*mixta* Latreille
*moori* Pinhey (from PINHEY, 1981)
*nigroflava* Martin
*palmata* Hagen
*persephone* Donnelly
*petalura taiyal* Asahina (♀ only)
*rileyi* Calvert
*rufipes* Ris (♀ only)
*septentrionalis* Burmeister
*serrata osiliensis* Mierzejewski
*sitchensis* Hagen
*subarctica* Walker
*subpupillata* McLachlan (from PINHEY, 1981)
*tuberculifera* Walker
*umbrosa* Walker (incl. ssp. *occidentalis* Walker)
*verticalis* Hagen
*viridis* Eversmann
*walkeri* Kennedy

*AESHNA (HESPERAESCHNA)* COCKERELL
*biliosa* Kennedy
**californica* Calvert
*canadensis* Walker
*confusa* Rambur
*cornigera* Brauer (incl. ssp. *planaltica* Calvert)
*dugesi* Calvert
*haarupi* Ris
*marchali* Rambur

*psilus* Calvert
*punctata* Martin
*variegata* Fabricius (incl. *A. peralta* Ris)
*williamsoniana* Calvert (♀ only)
*AESHNA (MARMARAESCHNA)* CALVERT
*brevifrons* Hagen
**intricata* Martin
*vigintipunctata* Ris
*AESHNA (NEURECLIPA)* NAVAS
**bonariensis* Rambur
*diffinis* Rambur (incl. ssp. *absoluta* Calvert)
*elsia* Calvert
*AESHNA (RHIONAESCHNA)* FÖRSTER
**maita* Förster (from CALVERT, 1956)
*AESHNA (SCHIZURAESCHNA)* CALVERT
*jalapensis* Williamson
**multicolor* Hagen
*mutata* Hagen
*AMPHIAESCHNA* SELYS
**ampla* (Rambur)
*ANACIAESCHNA* SELYS
*isoceles* (Müller) (= *isosceles* Lucas)
**jaspidea* (Burmeister)
*ANAX* LEACH
*imperator mauricianus* Rambur
*longipes* Hagen
*CASTORAESCHNA* CALVERT
**castor* (Brauer)
*coronata* (Ris) (♂ only)
*decurvata* Dunkle & Cook
*januaria* (Hagen) (♂ only)
*longfieldae* (Kimmins) (♂ only)
*CORYPHAESCHNA* WILLIAMSON
*adnexa* (Hagen)
**ingens* (Rambur)
*luteipennis* (Burmeister)
*perrensi* (McLachlan) (♂ only)
*rufipennis* (Kennedy) (♂ only)
*viriditas* Calvert
*HEMIANAX* SELYS
**ephippiger* (Burmeister)
*papuensis* (Burmeister)
*INDAESCHNA* FRASER
**grubaueri* (Förster) (from FRASER, 1926)
*OREAESCHNA* LIEFTINCK
**dictatrix* Lieftinck
*dominatrix* Vick & Davies

## CHARACTERISTICS DOCUMENTED

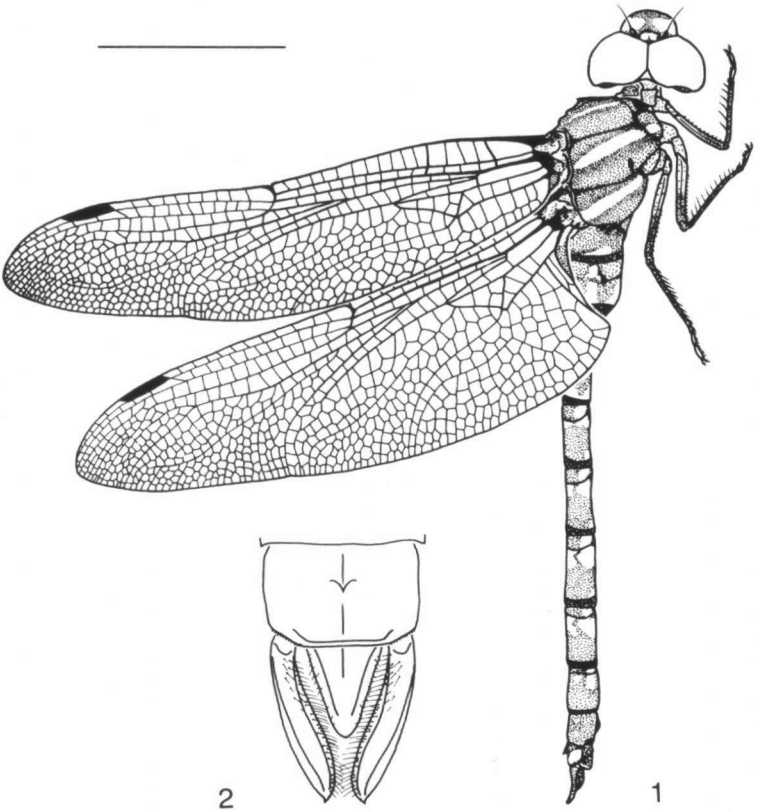
Most of the characteristics documented are standard items in dragonfly taxonomy and need no explanation. An important exception is the lateral abdominal carinae.

Submarginal ventral carinae usually form, or lie just below, the lateral margins of the abdominal tergites in aeshnids. Dentate, they commonly mark the fold where the tergite bends back towards the sternite on the underside of the abdomen. On segment 9, however, their presence is variable. In some species, they are well developed, continuing from the line of the ventral carinae of segment 8; in others, they are poorly developed, evident as folding or dentation for only part of the segment length; and in a few they are vestigial or absent, sometimes being replaced by supplementary lateral carinae or ridges, often present on more anterior abdominal segments. These supplementary lateral ridges are widespread in the aeshnids that form the subject of this paper, and can coexist with submarginal ventral carinae.

## THE SUBDIVISIONS OF THE AESHNINAE

DAVIES & TOBIN (1985) divided the Aeshninae into four tribes, the Aeshnini, Anactini, Gynacanthagini, and Polycanthagini. For convenience, their scheme is adopted here. The Gynacanthagini and Polycanthagini are distinctive groups, and lie outside the scope of this paper. The Aeshnini and Anactini, however, are similar in many ways, the main features used to distinguish them being:

(1) The anal margin of the hindwing is angulated in male Aeshnini and the associated auricle is well developed, whereas in male Anactini the base of




Figs 1-2. Male *Aeshna brevistyla* (W. Australia): (1) lateral view; – (2) anal appendages, dorsal view. – [Scale line = 15 mm (Fig. 1), ca 3.8 mm (Fig. 2).]

the hindwing is rounded and the auricle is vestigial (except in *Anaciaeschna*).

(2) The distal course of $R_3$ (Tillyard-Fraser notation) is uniformly curved in the Aeshnini, but kinked forward behind the pterostigma in the Anactini (cf. FRASER, 1957; DAVIES & TOBIN, 1985).

These character-states suggest derived status for the Anactini.

The tribe Aeshnini includes six genera: *Aeshna* (with six subgenera, *Aeshna, Hesperaeschna, Marmaraeschna, Neureclipa, Rhionaeschna* and *Schizuraeschna*), *Amphiaeschna, Castoraeschna, Coryphaeschna, Indaeschna* and *Oreaeschna*. Three genera are usually placed in the Anactini: *Anaciaeschna, Anax* and *Hemianax*. However, as its name implies, *Anaciaeschna* appears to be annectant between the two tribes, as the male has an angulated anal margin and an

auricle, but $R_3$ is kinked forward behind the pterostigma in the type species. I have, therefore, included it in this analysis.

## NOTES ON *AESHNA BREVISTYLA*

*Aeshna brevistyla* is a boldly-patterned, dark brown, yellowish green and blue dragonfly with short anal appendages (Figs 1-2). TILLYARD (1916) gave an extensive redescription of it, but a few points need emphasis here.

V e n a t i o n. – Triangular spaces crossed; forewing triangle more elongate than hind (Fig. 3). Anal loop 3 cells wide (Fig. 16). Anal triangle 3-celled, ending before the anal angle, the longitudinal vein meeting crossvein at or near inner margin of triangle (Fig. 6). $R_3$ strongly bowed behind pterostigma (Figs 22-23); fork of $IR_3$ near (forewing) or basal to (hindwing) level of base of pterostigma, asymmetrical, enclosing 2-4 rows of cells, the anterior branch weak, zig-zagged, separated from $R_3$ by ill-defined row of 1-2 cells(Figs 22-23). Median space free (Fig. 1).

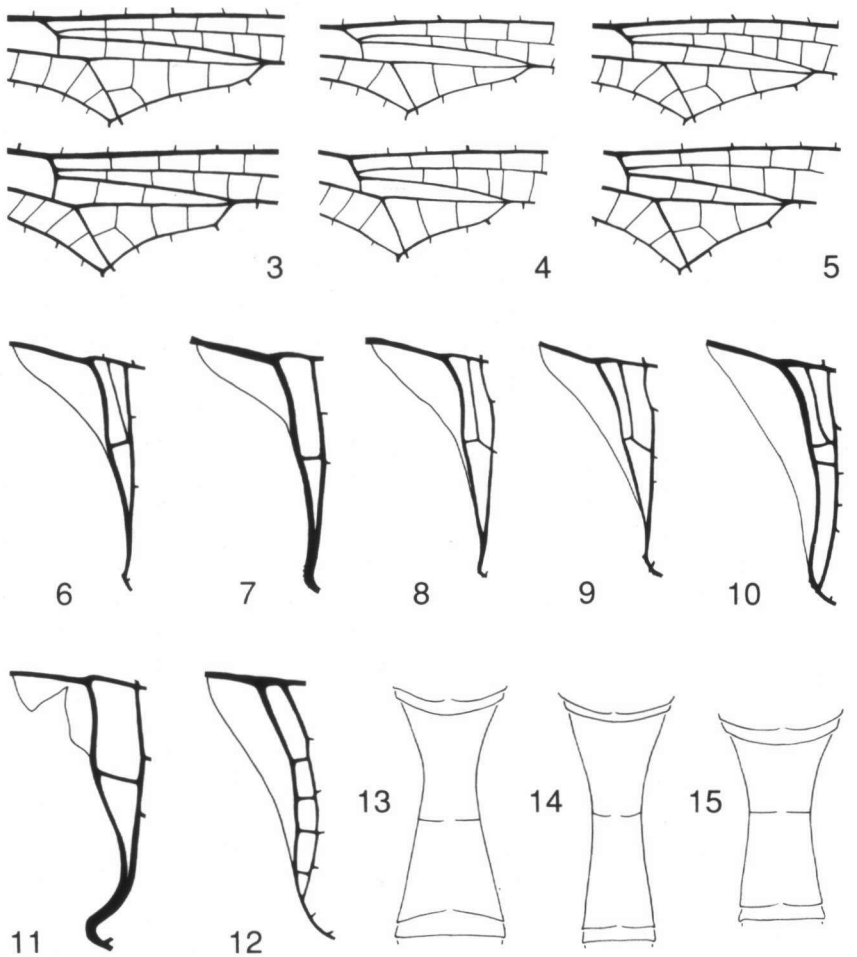
A b d o m e n. – Sternite 1 simple, not dentate (Fig. 40); posteroventral corners of tergite 1 broadly rounded (Fig. 40). Supplementary lateral keels well developed on tergite 9 of the male, less well developed on segments 6-8; ventral carinae much reduced on tergite 9 (Fig. 50). Superior appendages of male short, simple, tergite 10 bearing dorsal spine (Fig.2); anal appendages of female short. Dentigerous plate not developed, posterior margin of segment 10 simple, lower surface of segment dentate (Fig. 48).

## THE SUBGENERA OF *AESHNA*

CALVERT (1956) summarised the criteria on which the subgeneric division of *Aeshna* depends.

(1) The five subgenera confined to the New World differ from *Aeshna* sens. str. in having a prominent denticulate or hairy tubercle on abdominal sternite 1 (Fig.41). The tubercle is low in *A. (M.) vigintipunctata* and may be poorly developed in the female. In most species of typical *Aeshna* sternite 1 is simple. Exceptions occur: in, e.g., *A. rileyi* the sternite is dentate but not swollen (Fig. 42); in *A. interrupta* it has a dentate centre and hind margin (Fig. 43), whereas in some other species, e.g. *A. juncea americana, A. mutata* and *A. tuberculifera* there is a slight hummock (Fig. 44), strongly dentate in *A. minuscula* (Fig. 45).

(2) *Neureclipa* differs from the other four New World subgenera primarily through having the hypertriangle free (Fig. 4) (occasionally crossed in *A. diffinis*, rarely so in *A. bonariensis*) and the anal loop with two rows of cells across the wing (Fig. 4) (sometimes three cells along posterior margin, or with third, central cell) (Fig.16). In *Hesperaeschna, Marmaraeschna,*



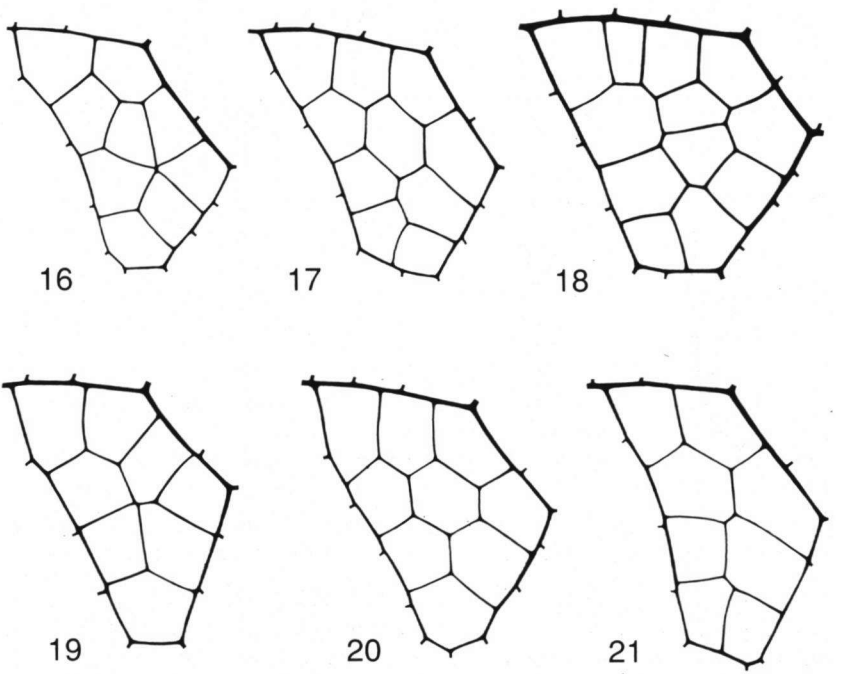

Figs 3-15. 3-5, Triangular region of fore- and hindwing: (3) *Aeshna brevistyla* ♂ (Williams, W. Australia); – (4) *Aeshna bonariensis* ♂ (Ciudad Universitaria, Buenos Aires, Argentina); – (5) *Aeshna confusa* ♂ (Pelotas, Rio Grande do Sul, Brazil). – 6-12, Anal triangle of ♂: (6) *Aeshna brevistyla* (Williams, W. Australia); – (7) *Aeshna grandis* (Karlsruhe, Germany); – (8) *Aeshna mixta* (Lage Vuursche, Netherlands); – (9) *Anaciaeschna jaspidea* (Berrimah, N.T., Australia); – (10) *Anaciaeschna isoceles* (Karlsruhe, Germany); – (11) *Castoraeschna castor* (Rio de Janeiro, Brazil); – (12) *Anax longipes* (Gainesville, FL, U.S.A.). – 13-15, Abdominal segment 3, ♂, dorsal view: (13) *Aeshna brevistyla* (Williams, W. Australia); – (14) *Anaciaeschna jaspidea* (Berrimah, N.T., Australia); – (15) *Anaciaeschna isoceles* (Karlsruhe, Germany).

*Rhionaeschna* and *Schizuraeschna* the hypertriangle is crossed, usually by several veins, and the anal loop commonly has three rows of cells, usually with a more conspicuous central cell or cells (Figs 5, 17). However, two rows of cells have been recorded in the anal loops of some species belonging to these subgenera, sometimes only in one wing, and *A. californica*, the type species of *Hesperaeschna*, commonly has two rows. (So does at least one typical *Aeshna*, *A. mixta*.) *Aeshna "peralta"* intergrades from *Hesperaeschna* to *Neureclipa* in both characters.

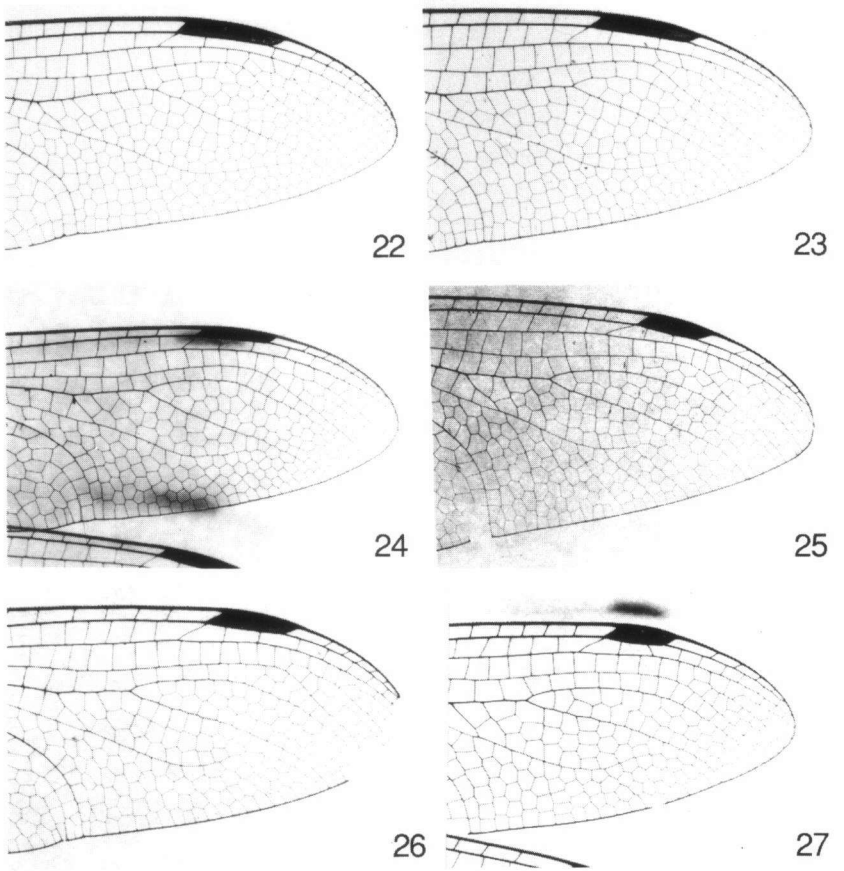
(3) *Schizuraeschna* is distinguished from the other subgenera primarily in having the male superior appendages bifid towards the tip.

(4) *Hesperaeschna* and *Rhionaeschna* appear to be closely allied (CALVERT, 1956), and may not be separable.

(5) *Hesperaeschna* and *Marmaraeschna* differ mainly in synthoracic coloration: in *Hesperaeschna*, the mes- and metepimeron bear pale stripes (reduced to spots in *A. biliosa* and markedly lobed in *A. cornigera planaltica* and *A. haarupi*), whereas *Marmaraeschna* has the synthorax patterned




Figs 16-21. Anal loop of ♂: (16) *Aeshna bonariensis* (Ciudad Universitaria, Buenos Aires, Argentina); – (17) *Aeshna confusa* (Pelotas, Rio Grande do Sul, Brazil); – (18) *Aeshna eremita* (Overflowing River, MB, Canada); – (19) *Aeshna brevistyla* (Stratford, Vic., Australia); – (20) *Aeshna brevistyla* (Williams, W. Australia); – (21) *Anaciaeschna jaspidea* (Humpty Doo, N.T., Australia).



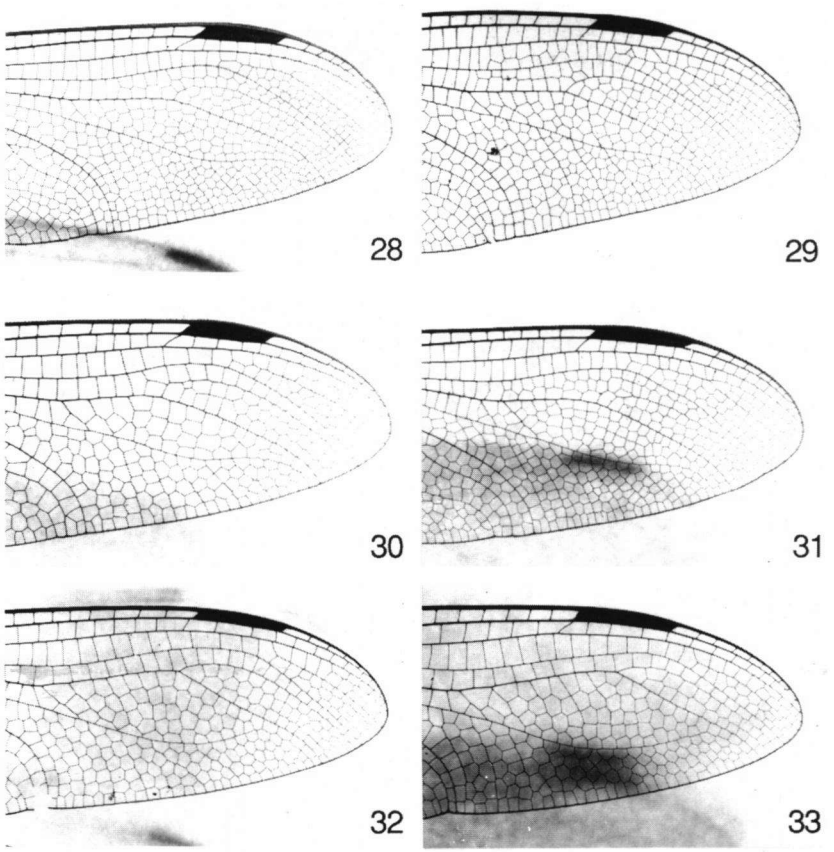

Figs 22-27. Venation in apical part of wing, *Aeshna* (forewing, unless otherwise indicated): (22-23) *Aeshna brevistyla* ♂ (Williams, W. Australia), ♀ (Millstream Station, W. Australia); – (24) *Aeshna minuscula* ♂ (Giant's Castle National Park, Natal, South Africa); – (25) *Aeshna confusa* ♂ (hindwing) (Pelotas, Rio Grande do Sul, Brazil); – (26) *Aeshna bonariensis* ♂ (Ciudad Universitaria, Buenos Aires, Argentina); – (27) *Aeshna diffinis* ♂ (Contulmo, Prov. Arauco, Chile). [Not to scale]

"with scattered black or brown marks" (CALVERT, 1956). [The name is derived from the Greek *marmaros*, marbled (CALVERT, 1952).]

However, other characteristics relevant to the placement of *Aeshna brevistyla* do not correlate with these subgeneric divisions. Points common to most or all species of *Aeshna* include:

(1) The triangles and, commonly, the subtriangles are crossed (Figs 3,5).

(2) The anal triangle has 2-3 cells (Figs 6-8).




Figs 28-33. Venation in apical part of forewing: (28) *Aeshna caerulea* ♂ (Jokkmokk, Sweden); – (29) *Aeshna grandis* ♀ (Karlsruhe, Germany); – (30) *Aeshna juncea americana* ♂ (Nordegg, AB, Canada); – (31) *Aeshna septentrionalis* ♀ (Great Caribou Island, Newfoundland, Canada); – (32) *Castoraeschna castor* ♂ (Rio de Janeiro, Brazil); – (33) *Coryphaeschna ingens* ♂ (Fisheating Creek, FL, U.S.A.). [Not to scale]

(3) The median space is free (Fig. 1).
(4) The dentigerous plate of the female consists of a dentose area on the posteroventral margin of an otherwise unmodified segment 10 (Figs 48-49).
(5) Abdominal segment 3 is markedly constricted (Fig. 13).
(6) Abdominal segment 10 usually bears a dorsal carina in the male, forming a low to well marked dorsal ridge to spine (Figs 2, 50-53) (absent in species of *Aeshna* sens. str. with a ventral, subterminal spine on the superior

appendage – *A. arida, A. constricta, A. palmata, A. persephone, A. umbrosa* and *A. walkeri* – and also in the African species *A. minuscula*).

Some character-states are variable but, apparently, not in accord with the existing subgeneric divisions.

(1) At least in *Aeshna* sens. str., *A. (Hesperaeschna)* (Fig. 51) and *A. (Schizuraeschna)*, but not in *Aeshna brevistyla*, the lateral regions of tergites 5- or 6-8 are variably buckled but not keeled; keels are better developed in *Aeshna brevistyla* (Fig. 50) and best so in species of *A. (Neureclipa)* (Fig. 52). Only in *Aeshna brevistyla* is the supplementary lateral keel well developed on tergite 9; it is at most weakly developed in other groups of *Aeshna*, accompanied by variable atrophy of the submarginal ventral carina, which is intact in some species [e.g., *A. (H.) confusa, A. (H.) variegata* (Fig. 51) and *A. (A.) palmata*, but not in A. (H.) *canadensis*]; reduced to ca half the segment length in others [e.g. *A. (A.) grandis* (Fig. 53)]; and weak or atrophied in the remainder [e.g., *A. (H.) canadensis* and the species of typical *Aeshna, A. eremita, A. minuscula* and *A. rileyi*].

(2) The distal course of $R_3$ and $IR_3$ is also variable. In most species of all subgenera, $R_3$ is evenly curved and the fork of $IR_3$ is well marked and more or less symmetrical. $R_3$ and the anterior branch of $IR_3$ are separated by a single row of cells (Fig. 24). However:

(a) $R_3$ is slightly buckled in some species, with or without double cells between $R_3$ and $IR_3$ [as, e.g., in *A. (H.) confusa, A. (N.) bonariensis* and *A. (N.) diffinis* (Figs 25-27)].

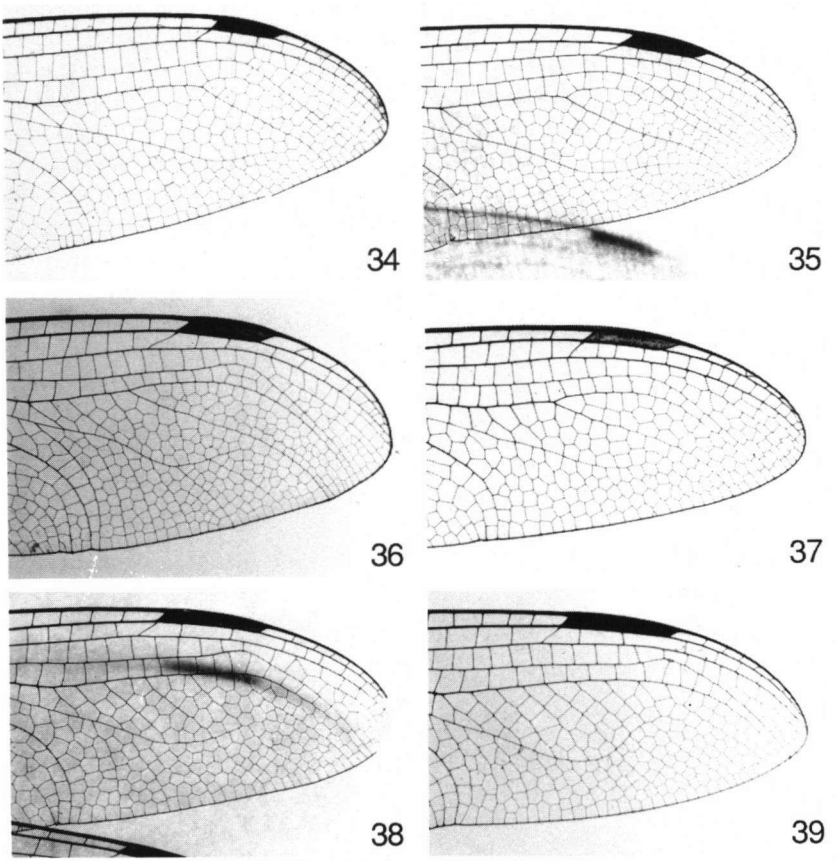
(b) $IR_3$ is markedly asymmetrical in several species of typical *Aeshna*, sometimes associated with proliferation of cells [e.g., *A. caerulea* (Fig. 28), *A. grandis* (Fig. 29); some *A. juncea* (Fig. 30) and *A. septentrionalis*].

(c) In a few *A. (A.) septentrionalis*, $R_3$ is strongly bent behind the pterostigma, and the anterior branch of $IR_3$ is weakened (Fig. 31).

## CHARACTERISTICS OF OTHER AESHNINI

### *AMPHIAESCHNA*

In the Javanese aeshnid *Amphiaeschna ampla* the median space is crossed by 3-5 veins; the triangle is elongate and it and the hypertriangle are crossed, the latter by 4-6 veins; the anal triangle is 3-celled; and $R_3$ is evenly curved, with one row of cells between it and the symmetrical fork of $IR_3$. Abdominal sternite 1 lacks a tubercle but has in its place a slight, denticulate swelling; the dentigerous plate projects slightly; and there is no dorsal spine on abdominal segment 10 of the male. I have no data on the lateral abdominal keels or submarginal ventral carinae.

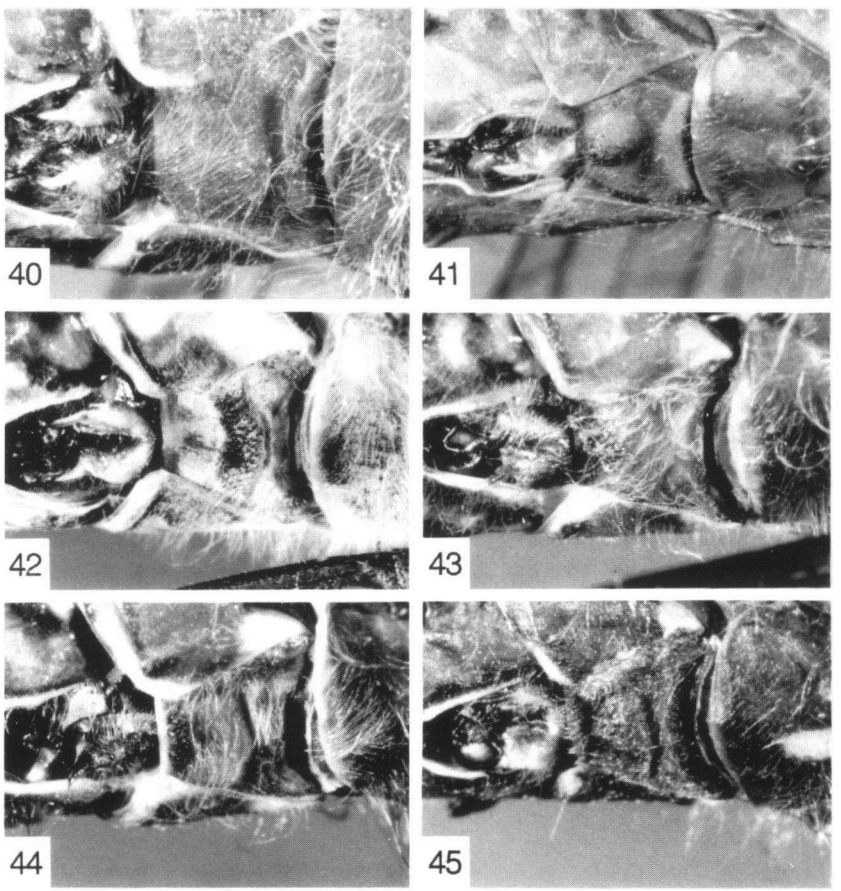



Figs 34-39. Venation in apical part of forewing: (34) *Oreaeschna dictatrix* ♂ (Ok Sibil Valley, south-central New Guinea); – (35) *Oreaeschna dominatrix* ♂ (New Caledonia); – (36) *Anaciaeschna jaspidea* ♂ (Berrimah, N.T., Australia); – (37) *Anaciaeschna isoceles* ♂ (Karlsruhe, Germany); – (38) *Anax imperator mauricianus* ♂ (Rustfontein, O.F.S., South Africa); – (39) *Hemianax ephippiger* ♂ ("Annaimallai Hills", Kerala, India). [Not to scale]

*CASTORAESCHNA*

This South American genus is unique in having the posteroventral corners of abdominal tergite 1 produced into a narrow flap which curves over the sternite which, in turn, bears a strongly swollen tubercle (*C. castor*, *C. januaria*, *C. longfieldae*) (Fig. 46), or a low, hirsute hummock (*C. coronata*, *C. decurvata*). All species examined, except *C. lonfieldae*, have $R_3$ evenly curved, separated by one row of cells from $IR_3$, which is evenly and strongly forked (Fig. 32). In *C.*

*longfieldae* $R_3$ is slightly bent. The triangle and hypertriangle are crossed but the median space is free; the anal triangle is 2-celled and the anal angle is pronounced (Fig. 11). The dentigerous plate of the female projects slightly, and is strongly dentate. Abdominal segment 10 of the male has (*C. coronata*) or lacks a dorsal spine (*C. castor*, *C. colorata*, *C. decurvata*, *C. januaria*, *C. longfieldae*). In the male of *C. castor* the submarginal ventral carina is poorly developed on segment 8 and reduced to anterior and posterior vestiges on segment 9, and weak supplementary ridges form the lateral boundaries of the segments.




Figs 40-45. Abdominal sternite 1, ♂, lateroventral view: (40) *Aeshna brevistyla* (Williams, W. Australia); – (41) *Aeshna bonariensis* (Ciudad Universitaria, Buenos Aires, Argentina); – (42) *Aeshna rileyi* (Royal National Park, Natal, South Africa); – (43) *Aeshna interrupta* (Powell Co., MT, U.S.A.); – (44) *Aeshna juncea americana* (Nordegg, AB, Canada); – (45) *Aeshna minuscula* (Giant's Castle National Park, Natal, South Africa).

### *CORYPHAESCHNA*

Like *Castoraeschna*, *Coryphaeschna* differs in several ways from *Aeshna* sens. lat. (including *A. brevistyla*). In particular, the fork of $IR_3$ is almost parallel-sided, or tapers to the termen, and encloses only two rows of cells (Fig. 33), as in *Anax* and *Hemianax* (sometimes a third row is present near the wing margin and, in *C. viriditas*, the central region of the field may be swollen, with a third row). $R_3$ is evenly curved, with one row of cells between it and the anterior branch of $IR_3$ (Fig. 33).

The anal triangle is 2-celled, and the anal angle is prominent; the triangle and hypertriangle are crossed but the subtriangle is usually free except (rarely) in *C. ingens* and (more commonly) in *C. viriditas*, where it may be crossed in either or both wings; and the median space in *C. viriditas* is occasionally crossed.

Abdominal sternite 1 is flat; the dentigerous plate projects but is short and heavily spined; and the male lacks the dorsal spine on abdominal segment 10. The male of *C. ingens* has well developed submarginal ventral carinae on segments 8 and 9, and supplementary lateral ridges are absent.

### *INDAESCHNA*

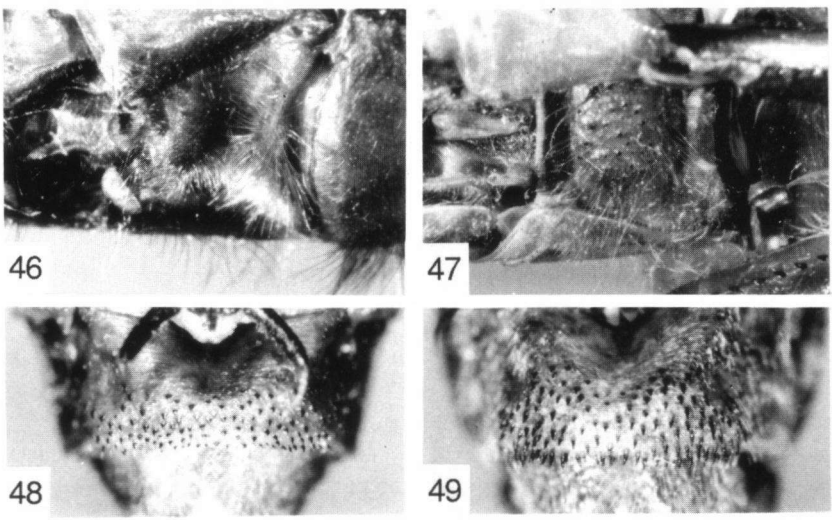
According to FRASER (1926), *Indaeschna* is allied to *Amphiaeschna* and, like it, has the median space crossed. At least in *I. grubaueri*, the type species, the female has a long dentigerous plate.

### *OREAESCHNA*

*Oreaeschna* is an enigmatic genus. It shows some character-states that indicate it is aeshnine; others that LIEFTINCK (1937) thought might indicate affinities with the Anactini; and some that are autapomorphic.

The median space is free; the triangles and hypertriangles are crossed, the latter by 3-4 veins; the anal triangle is 3- or 4-celled, ending well before the anal angle (LIEFTINCK, 1937, fig. 46); the anal loop is broad, up to 4 cells wide; $R_3$ is bent behind the pterostigma, slightly in *O. dominatrix*, particularly in the hindwing, more strongly so in *O. dictatrix* in which it resembles the state shown by *Aeshna brevistyla*, with one row of cells, or some double cells, separating it from the weak anterior branch of the asymmetrical fork of $IR_3$ (Figs 34-35); in the female of *O. dictatrix*, the wing bases are tinged dark rusty brown to or beyond $Ax_1$.

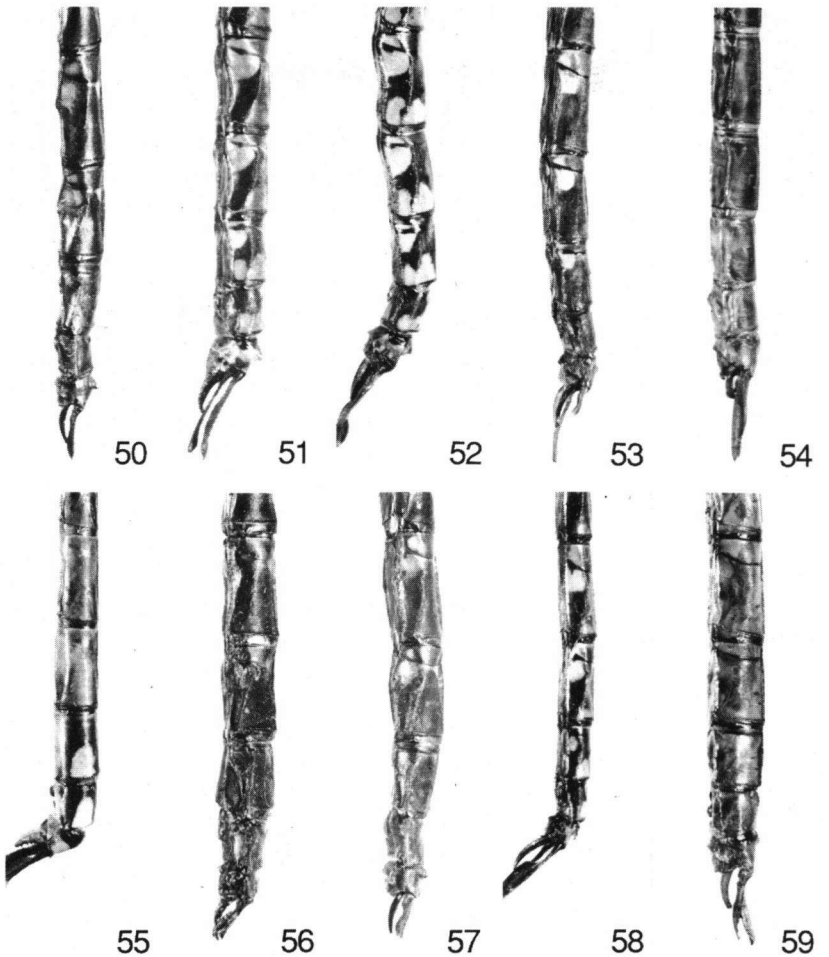
Abdominal sternite 1 lacks a tubercle; the dentigerous plate of the female is undeveloped, the underside of segment 10 being covered with small denticles; and abdominal segment 10 of the male lacks (*O. dictatrix*) or possesses (*O. dominatrix*) a dorsal spine (Figs 56-57).




Figs 46-49. 46-47, Abdominal sternite 1, ♂, lateroventral view: (46) *Castoraeschna castor* (Rio de Janeiro, Brazil); – (47) *Anaciaeschna isoceles* (Karlsruhe, Germany); – 48-49, Dentigerous plate of ♀, ventral view: (48) *Aeshna brevistyla* (Millstream Station, W. Australia); – (49) *Aeshna umbrosa* (Cleveland, OH, U.S.A.).

The most remarkable feature of *Oreaeschna* is the stout abdomen, very strongly constricted at segment 3 in the male, less so in the female (cf. LIEFTINCK, 1937, fig. 46; VICK & DAVIES, 1990, fig. 1), then expanded on segments 4-5 and 8-9. This expansion is accompanied by the strong development of supplementary lateral carinae, particularly on segments 7-9 in the male, with slight development on segment 6, and on 7-8 in the female with slight development on 9 (*O. dictatrix*) or on 8, with slight development on 9 (*O. dominatrix*). Submarginal ventral carinae are well developed on segments 7-8 in both sexes, but those on segment 9 of males are all but vestigial (Figs 56-57), somewhat less developed than in *Aeshna brevistyla* (Fig. 50). The superior anal appendages are short, slender, convergent, similar in length to the broad-based inferior appendage (Figs 56-57; cf. LIEFTINCK, 1937, fig. 47; VICK & DAVIES, 1990, fig. 2); in other words, much shorter than in other Aeshnini, including *Aeshna brevistyla*.

LIEFTINCK (1937) commented that the supplementary lateral keels of *Oreaeschna* are reminiscent of those in the Anactini. However, the occurrence of less-well developed keels on the same abdominal segments of *Aeshna brevistyla*, and in many other species of *Aeshna* sens. lat., suggests aeshnine affinity, as venation indicates (cf. LIEFTINCK, 1937). The extensive development of keels on *Oreaeschna* is linked to the marked flattening of the abdomen, and is




Figs 50-59. Abdominal segments 5-10, ♂, lateral view: (50) *Aeshna brevistyla* (New Caledonia); – (51) *Aeshna variegata* (Rio Tres Brazos, Prov. Magallanes, Chile); – (52) *Aeshna diffinis* (Contulmo, Prov. Arauco, Chile); – (53) *Aeshna grandis* (Karlsruhe, Germany); – (54) *Anax longipes* (Alachua Co., FL, U.S.A.); – (55) *Hemianax ephippiger* (Wolwespruit, O.F.S., South Africa); – (56) *Oreaeschna dictatrix* (Ok Sibil Valley, south-central New Guinea); – (57) *Oreaeschna dominatrix* (New Caledonia) (abdomen slightly twisted); – (58) *Anaciaeschna jaspidea* (Viti Levu, Fiji); – (59) *Anaciaeschna isoceles* (Karlsruhe, Germany). [Not to scale]

unrelated to the well developed keels on most abdominal segments of male *Anax* (which are lacking in males of both species of *Hemianax*) (Figs 54-55).

## THE GENUS *ANACIAESCHNA*

SCHMIDT (1950) transferred *isoceles* (as *isosceles*) from *Aeshna* to *Anaciaeschna* (type species *A. jaspidea*). These two sandy-coloured species differ sufficiently to cast doubt on their congeneric status, an issue that depends on the characteristics of the other species of *Anaciaeschna* (see DAVIES & TOBIN, 1985), and lies outside the scope of this paper; but it is best to document the two species separately.

### *ANACIAESCHNA JASPIDEA*

*Anaciaeschna jaspidea* shows one of the hallmarks of the Anactini, the sharp kink in $R_3$ behind the pterostigma (Figs 38-39), commonly with 2 rows of cells between $R_3$ and the anterior branch of $IR_3$ at the kink (Fig. 36). It is much sharper than the bow in $R_3$ shown by any of the species of Aeshnini examined (cf. Figs 22-33), even *A. brevistyla*.

The fork of $IR_3$ is distinct, the posterior branch diverging from the almost straight anterior, enclosing ca 4 rows of cells (Fig. 36); the conspicuous, posteriorly-directed forks from $IR_3$, characteristic of *Anax* and *Hemianax*, are lacking. The median space is free; the triangle and hypertriangle are crossed, the subtriangle free; the anal triangle is 3-celled, ending at the anal angle (Fig. 9); the anal loop has 2 rows of cells (Fig. 21) or, more commonly, a central, third cell.

Abdominal sternite 1 is slightly swollen and dentate; abdominal segment 3 is slender and constricted (Fig. 14); the dentigerous plate is like that in *Aeshna* sens. lat., a dentate area on the posteroventral margin of an otherwise unmodified sternite 10; and the male has a low dorsal spine on abdominal segment 10. Abdominal segments 4-9 show distinct lateral buckling in the male, but not lateral carinae, and segment 9 has a strong submarginal ventral carina, not dentate (Fig. 58).

### *ANACIAESCHNA ISOCELES*

The distal course of $R_3$ is unlike that in *A. jaspidea*, *Anax* or *Hemianax*, showing only slight curvature (Fig. 37; cf. Figs 38-39). The fork of $IR_3$ is more symmetrical than in *A. jaspidea*, separated from $R_3$ by a single row of cells, and there are commonly 3 rows of cells between the arms of the fork. As in *A. jaspidea*, there is no repetitive forking of $IR_3$. The median space is free, the triangular spaces crossed. The anal triangle is 4-celled, its distal vein reaching the termen beyond the anal angle (Fig. 10). The anal loop includes 2-3 rows of cells. It is also worth noting that the rib veins in the anal field are well developed, including a strong fork at the end of 1A.

Abdominal sternite 1 is more swollen in the midline than in *A. jaspidea*, and

dentate (Fig. 47); abdominal segment 3 is stout, moderately constricted (Fig. 15); the dentigerous plate is as in *Aeshna* sens. lat.; and segment 10 lacks a dorsal spine in the male. The abdominal tergites of the male are almost unbuckled, and tergite 9 has a strong, dentate submarginal ventral carina, continuing from the line of that on segment 8 (Fig. 59).

## DISCUSSION

This comparison between *Aeshna brevistyla* and its congeners confirms its taxonomic isolation, except from *Oreaeschna*. *A. brevistyla* lacks a tubercle on abdominal sternite 1; the superior appendages of the male are short and simple; and the hypertriangle is crossed. This combination of character-states distances it from the American subgenera of *Aeshna*, as does its radial venation – $R_3$ strongly bowed behind the pterostigma, and the anterior fork of $IR_3$ poorly defined. Such radial venation (and superior appendages) similarly distances it from species of the subgenus *Aeshna* except some *A. septentrionalis* (and, perhaps, its Old World relative, *A. caerulea*), in which the radial venation can be similar.

There do not appear to be closer similarities between *Aeshna brevistyla* and most other genera of Aeshnini or Anactini. The lack of median cross-venation separates it from *Amphiaeschna* and *Indaeschna*; the radial venation from all other genera except *Oreaeschna*; the unelaborated dentigerous plate from *Castoraeschna* and *Coryphaeschna*; the lack of elaboration on abdominal tergite 1 from *Castoraeschna*; and the shape of the fork in $IR_3$ from *Coryphaeschna*. The highly specialised abdomen of *Oreaeschna* distinguishes it from *Aeshna brevistyla*.

The conclusion that *Aeshna brevistyla* is closely related to existing South American aeshnids (whether congeners or not) cannot be sustained. *A. brevistyla* can no longer be viewed as a survivor from Gondwana. It is not allied to *Anaciaeschna*, whether or not *isoceles* is included, or to *Amphiaeschna* or *Indaeschna*. The similarity of the radial venation and the secondary specialisation of basically similar supplementary lateral abdominal keels suggest that *Oreaeschna* is allied to *Aeshna brevistyla*, as VICK & DAVIES (1990) indicated. In addition, the appearance of New Caledonian *Aeshna brevistyla* is strikingly similar to that of *Oreaeschna dominatrix* (VICK & DAVIES, 1990). *Oreaeschna* can be interpreted as a south-west Pacific offshoot of *Aeshna* into an environment otherwise devoid of Aeshnini (cf. VICK & DAVIES, 1990). However, although a possible forerunner of *Oreaeschna, Aeshna brevistyla* is basically a species of *Aeshna* sens. lat., representing an Antipodean subgenus of a genus otherwise widely distributed in the Holarctic region, the neotropics, Asia and Africa. Its origins thus remain enigmatic, as they do for the Australian megapodagrionids, amphipterygids and, perhaps, brachytronine aeshnids.

*AESHNA (ADVERSAESCHNA*)* SUBGEN. NOV.

**Type species:** *Aeschna brevistyla* Rambur, 1842.

Triangular spaces crossed; forewing triangle more elongate than hind; anal loop 3 cells wide. Anal triangle 3-celled, ending before the anal angle, the longitudinal vein meeting crossvein at or near inner margin of triangle. $R_3$ strongly bowed behind pterostigma; fork of $IR_3$ near (forewing) or basal to (hindwing) level of base of pterostigma, asymmetrical, enclosing 2-4 rows of cells, anterior branch weak, zig-zagged, separated from $R_3$ by ill-defined row of 1-2 cells; median space free.

Abdominal sternite 1 simple, not dentate; posteroventral corners of tergite 1 broadly rounded. Superior appendages of male short, simple, tergite 10 bearing dorsal spine. Anal appendages of female short; dentigerous plate not developed, posterior margin of sternite 10 simple, its lower surface dentate. Abdominal tergites 7-9 of male with supplementary lateral carinae present as rounded ridges, best developed on segment 9 but also slightly evident on segment 6, the submarginal ventral carina of segment 9 reduced, particularly in the posterior half of the segment.

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## REFERENCES

CALVERT, P., 1952. New taxonomic entities in neotropical aeshnas (Odonata: Aeshnidae). *Ent. News* 63: 253-264.

CALVERT, P., 1956. The neotropical species of the "subgenus Aeschna" sensu Selysii 1883 (Odonata). *Mem. Am. ent. Soc.* 15: v, 1-251, Plates 1-47, Tables 1-19, Maps 1-7, i-iv.

DAVIES, D.A.L. & P. TOBIN, 1985. The dragonflies of the world. A systematic list of the extant species of Odonata Vol. 2. Anisoptera. *Soc. int. odonatol. rapid Comm.* (Suppl.) 5: x, 1-151.

FRASER, F.C., 1926. Notes on a collection of dragonflies (order Odonata) from the Dutch East Indies and descriptions of four new species from the neighbouring continent. *Treubia* 8: 467-494.

FRASER, F.C., 1957. *A reclassification of the order Odonata*. R. Zool. Soc. N.S.W., Sydney.

HOUSTON, W.W.K. & J.A.L. WATSON, 1988. Odonata. *Zool. Catal. Aust.* 6: 33-132, 283, 289-299.

LICHTENSTEIN, A.A.H., 1796. *Catalogus musei zoologici ditissimi Hamburgi, d III. Februar 1796. Auctionis lege distrahendi. Sectio tertia continens Insecta*. Schniebes, Hamburg.

* *Adversus*, opposite in physical position.

LIEFTINCK, M.A., 1937. The dragonflies (Odonata) of New Guinea and neighbouring islands Part IV. Descriptions of new and little known species of the families Agrionidae (sens. lat.), Libellulidae and Aeshnidae (genera Idiocnemis, Notoneura, Papuagrion, Teinobasis, Aciagrion, Bironides, Agyrtacantha, Plattycantha, and Oreaeschna). *Nova Guinea* (NS) 1: 283-364.

LIEFTINCK, M.A., 1954. Handlist of Malaysian Odonata. *Treubia* 22 (Suppl.): xiii, 1-202.

MARTIN, R., 1908. Aeschnines. *Collns zool. de Sélys-Longchamps* 18: 1-84, pls 1-2.

MARTIN, R., 1911. Odonata Fam. Aeschnidae Subfam. Aeschninae. *Genera insectorum* 115: 1-34.

NEEDHAM, J.G. & M.J. WESTFALL, 1955. *A manual of the dragonflies of North America (Anisoptera).* Univ. California Press, Berkeley-Los Angeles.

PINHEY, E.C.G., 1952. *The dragonflies of southern Africa.* Transvaal Mus., Pretoria.

PINHEY, E.C.G., 1981. Two interesting species of Aeshna Fabricius from Zambia (Odonata: Aeshnidae). *Arnoldia, Zimbabwe* 9: 61-68.

RAMBUR, P., 1842. *Histoire naturelle des insectes. Névroptères.* Roret, Paris.

SCHMIDT, E., 1950. Was ist Libellula... isoceles O.F. Müller 1767? *Ent. Z.* 60: 1-9.

TILLYARD, R.J., 1916. Life-histories and descriptions of Australian Aeschninae; with a description of a new form of Telephlebia by Herbert Campion. *J. Linn. Soc.* (Zool.) 33 (222): 1-83.

WATSON, J.A.L., 1981. Odonata (dragonflies and damselflies). *In*: A. Keast, [Ed.], Ecological biogeography of Australia, pp. 1141-1167, Junk, The Hague.

VICK, G.S. & D.A.L. DAVIES, 1990. A new species of Oreaeschna from New Caledonia (Anisoptera: Aeshnidae). *Odonatologica* 19: 187-194.