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ODONATA OF THE CAYMAN ISLANDS: A REVIEW

R. R. Askew, Richard Prosser, and **Philip S. Corbet**

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ABSTRACT

Twenty seven species of Odonata are known to occur in the Cayman Islands, a small, low-lying island group located about 200 km northwest of Jamaica in the Caribbean Sea. ***Nehallenia minuta, Coryphaeschna viriditas, Idiatapha cubensis, Macrodiplax balteata,*** and ***Tramea onusta*** are recorded for the first time.

INTRODUCTION

The Cayman Islands are a group of three low-lying islands in the North Caribbean, between 19 and 20 degrees north and 79 and 82 degrees west (Fig. 1). Cayman Brac is the easternmost of the three, lying 192 km west of the southwestern tip of Cuba and 200 km northwest of Jamaica. Little Cayman is situated about eight km, and Grand Cayman a further 95 km, to the west of Cayman Brac. The largest and most densely populated island is Grand Cayman, approximately 37 km long from west to east and with a maximum breadth of about 11 km. The two smaller islands each measure about 21 km by 2.5 km. Grand Cayman and Little Cayman have an altitude barely exceeding 20 m. above sea level, but Cayman Brac rises to twice this height.

The islands are too small to have permanently running waters, but there are abundant more or less saline lagoons, dikes and mangrove swamps. Rainfall feeds freshwater pools which may persist long enough to provide a habitat for Odonata larvae, and some of these pools (cow wells) have been artificially created to water cattle; there is a tendency for all of these accumulations of rainwater to become increasingly saline the longer they persist.

Although, to our knowledge, no systematic attempt has been made to detect discontinuity among flying seasons of Odonata on the islands, no seasonality is evident from the records available to us. We note, however, that the year-round high temperatures, and normal absence of prolonged drought, probably permit continuous development of the aquatic stages, and that adults of many species can be seen at most times of year.

The foundations of our knowledge of Cayman Odonata were laid by an expedition from Oxford University in 1938 (Fraser, 1943) which recorded twelve species. Askew (1980) added five species to the islands' faunal list and later increased the total to 22 species (Askew, 1994). The last publication, however, does not include some unpublished observations by Prosser and these, together with findings made on two more recent visits to Grand Cayman by Askew in 1995 and 1997, make an updated review of the Odonata fauna of the islands desirable. Five species are here newly recorded for the Cayman Islands.

OBSERVATIONS

Unless specified otherwise, all observations cited below refer to adults. Two of us (Corbet and Prosser) are indebted to Dr. Dennis Paulson for valued help with identifying specimens.

ZYGOPTERA

LESTIDAE

Lestes spumarius (Selys)
Found commonly on Grand Cayman and Cayman Brac in 1938 (Fraser, 1943) but only single specimens have been noted subsequently (all on Grand Cayman): October 1963 (coll. C. R. Warren), August 1985 (Malaise trap), March 1997 (Mastic Trail).

COENAGRIONIDAE

Ischnura hastata (Say)
Recorded only from Grand Cayman where it is often common in rank vegetation on marshy

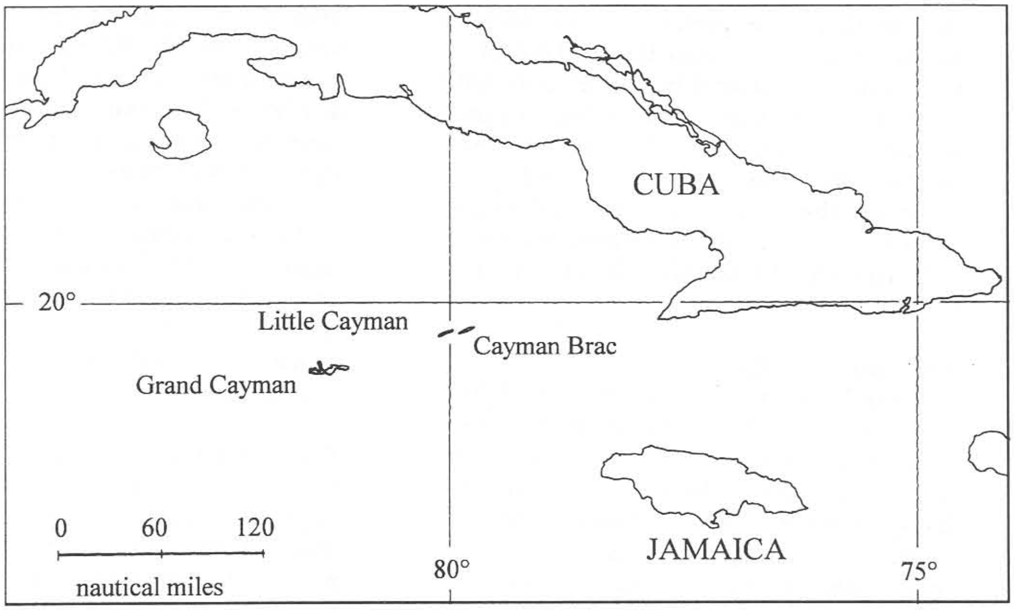

Figure 1. Map showing the location of the Cayman Islands

ground: October 1963 (coll. C. R. Warren), August 1975, April 1983, August 1985, February 1997.

Ischnura ramburii (Selys)
The surprising absence of this species from the 1938 Oxford University Expedition collection is commented upon by Fraser (1943). This species is, in fact, widespread on Grand Cayman, but has not yet been reported from the lesser Caymans. Females are dichromatypic, exhibiting homeochrome and heterochrome forms, the latter resembling the *aurantiaca* form of ***I. pumilio*** (Charpentier). Recorded as follows: October 1963 (coll. C. R. Warren), 1973, July 1975, December 1982, March, April, May and August 1983, August 1985, October 1995, February 1997.

Leptobasis vacillans Hagen in Selys
Less common than the two coenagrionids listed above and, like them, known only from Grand Cayman: April, August and October 1983, August 1985, August 1995, March 1997. The 1983 material was collected by Prosser in areas readily flooded by rain.

Nehalennia minuta (Selys)
Not previously recorded from the Cayman Islands. It was first collected by C. R. Warren at Red Bay, Grand Cayman in October 1963 and this material was identified in 1984 by D. R. Paulson. Subsequently, Prosser found the species in April and May 1983 at the Agricultural Ground and Askew found it in October 1995, February and March 1997 in the Botanic Park and on the Mastic Trail. Adults fly and perch low down in shaded vegetation growing in mud at the edges of drying pools.

ANISOPTERA

AESHNIDAE

Coryphaeschna viriditas Calvert (= *Coryphaeschna virens* Rambur)
Not previously recorded from the Cayman Islands. A specimen from Grand Cayman, identified by S. J. Brooks and now in the Natural History Museum, London, was found dead in a swamp pool at the transition between Buttonwood and Red Mangrove on 5 October 1983. Individuals of a large, green aeshnid were seen hawking along stretches of woodland edge in February 1997 at Botabano and in the Botanic Park, Grand Cayman. These were ***possible C. viriditas***, but two additional species of ***Coryphaeschna*** are found on Cuba and could also occur on the Cayman Islands. Lewis in Fraser (1943) expresses surprise that '***C. virens***' was absent from the 1938 Oxford University collection.

Anax amazili (Burmeister)
Anax are frequently seen hawking, and last-instar exuviae found, but uncertainty about whether

these are the present species or the next limits the number of reliable records that we have of the two species. ***A. amazili*** is reported from Little Cayman (2 females) and Grand Cayman (exuviae) by Fraser (1943), exuviae were collected on Grand Cayman in 1973 by P. Wagenaar Hummelinck (det. D. C. Geijskes), and a female was caught in a Mosquito Research and Control Unit (MRCU) light trap on Grand Cayman in 1985.

Anax junius (Drury)
All records are from Grand Cayman. Larvae were collected in May 1973 by Hummelinck and identified by D. C. Geijskes, two males were caught June and July 1983 by Prosser and two females in February 1997 by Askew. One of the females was captured with prey, a female ***Tramea abdominalis*** (Rambur). Observed to oviposit in tandem.

Gynacantha nervosa Rambur
Recorded only from Grand Cayman where it was first found in August 1980 when a female was taken at night in a lighted building. Another female was caught inside a house in July 1983, and a third female (apparently accompanied by a male, though not in tandem) was observed in February 1997 ovipositing in damp earth beneath trees in the Botanic Park, the flight of both insects being extremely difficult to follow as they flew in shade a few centimetres above the woodland floor.

Triacanthagyna septima (Selys)
A female was caught indoors at 10 a.m., Half Way Pond, George Town, Grand Cayman in January 1983 by Prosser, another female was found in a MRCU light trap in November 1983, and a third appeared indoors at midday in February 1984. Askew observed about eight individuals flying low in deep woodland shade on the Mastic Trail, October 1995. They were apparently feeding, but, as with ***G. nervosa***, very difficult to see because of their dull coloration in the poor light. Adults are crepuscular and oviposit in temporary forest pools.

LIBELLULIDAE

Micrathyria didyma (Selys)
Reported only from Grand Cayman in the Cayman Island (Fraser, 1943; Askew, 1994), this species is frequently about pools, dikes, and ditches, ranging from near-fresh to distinctly brackish, provided that there is abundant bushy vegetation nearby. Adult insects have been noted in almost every month. Males perch frequently and for long periods on twigs protruding from the water, and they hunt at a height of only about a metre amongst bushes. The white abdominal spot makes this an easily recognizable insect. Perhaps as a consequence of its relatively slow flight speed, ***M. didyma*** appears often to be the prey of larger dragonflies. In February 1997, a female was eaten by a female ***Erythemis vesiculosa*** (F.) and a male by a male ***E. plebeja*** (Burmeister).

Brachymesia furcata (Hagen)
Fraser (1943) records this species from all three Cayman Islands. On Grand Cayman it is abundant both on the coast and inland and probably flies throughout the year. Males perch for lengthy periods on twigs near water. Very large numbers of exuviae were attached to the aerophores of mangroves at the large, brackish lagoons behind the south coast. Females oviposit alone and one was seen (February 1997) to be grasped in tandem by a male ***Tramea abdominalis*** (Rambur).

Brachymesia herbida (Gundlach) (= *Cannacria herbida*)
Askew (1993) writes that larvae of ***B. herbida*** (identified by D. C. Geijskes) were found by P. Wagenaar Hummelink in May 1973 at two wells at Spot Bay, Cayman Brac. The first Cayman adults were found on Grand Cayman in February and March 1997, when two males were taken, and a third was seen, at a small freshwater pool at the edge of George Town. Adults perched frequently but briefly on the tips of twigs projecting from the water.

Orthemis "ferruginea (Fabricius)"
Found on Grand Cayman and Cayman Brac in 1938 (Fraser, 1943), and on Little Cayman in 1975 (Askew, 1980), this is an abundant dragonfly and adults have been observed in most months of the year. It seems to prefer more open areas near the larger pools and is infrequent along the dikes. [Antillean specimens referred to under the name *ferruginea* are currently being studied with a view towards establishing another species. ed.]

Erythemis plebeja (Burmeister) (= *Lepthemis plebeja*)
Recorded only from Grand Cayman, where it is uncommon, first by Fraser (1943) and subsequently by Askew (1994). It frequents fresh to brackish pools where males perch on prominent pieces of pool side vegetation, usually at a height of less than one meter. A male was found with ***Micrathyria didyma*** as prey. Females seen oviposited unguarded, one being watched for ten minutes as it flew ceaselessly and low over the surface of a pool, repeatedly dipping the tip of its abdomen beneath the water even though continually harried by male ***Brachymesia furcata***.

Erythemis simplicicollis (Say) (= *Lepthemis simplicicollis*)
An uncommon dragonfly recorded from Grand Cayman (Askew, 1994) where it is usually found beside larger or deeper ponds of relatively fresh water. Adults have been noted in February, June and August. Males patrol the margins of ponds, flying low and swiftly and seldom settling (reminiscent of male ***Orthetrum*** in Europe).

Erythemis vesiculosa (Fabricius) (= *Lepthemis vesiculosa*)
E. vesiculosa, like its two congeners (above), has been found only on Grand Cayman in the Cayman Islands, but there it is a very common and widespread dragonfly, probably throughout the year, on marshy ground or in the vicinity of pools, lagoons and dikes. It flies close to the ground, seldom over open water, and perches only briefly. A female was found with ***Micrathyria didyma*** as prey.

Erythrodiplax berenice naeva (Hagen)
Fraser (1943) writes that "this species must certainly be considered the most abundant form on all three of the Cayman Island". ***E. b. naeva*** is an Antillean form that has been treated as a species distinct from berenice of the United States (e.g. Needham & Westfall, 1955), but here we regard it as a subspecies. It is certainly very common, especially on beach ridges and about coastal lagoons, and it also penetrates, thought not so frequently, the interior of the islands. "This is the only truly salt-water dragonfly in North America. Its habitats (in Florida) are salt marshes and mangrove swamps along the coasts..." (Dunkle, 1989).

Erythrodiplax umbrata (Linnaeus)
Another very common species on all three islands but, unlike ***E. berenice***, it is most abundant near inland waters. Adults have been taken in every month. Fraser (1943) gives a detailed description of variation in wing pigmentation.

Erythrodiplax fervida (Erichson)
apparently this species is rare in the islands where it has been found only on Grand Cayman. A single female was taken in George town in August 1975 (Askew, 1980), two males were collected by Prosser in April and June 1983 at the Agricultural Ground, and a copulating pair was found in August 1985 beside a small, shallow rainwater pool on the outskirts of George Town. At this last site, during February 1997, one or two males were regularly observed over a two-week period close to a small pool, and they disappeared only when the pool completely dried out. These males were exceedingly alert and agile and escaped capture.

Idiataphe cubensis (Scudder)
A new record for the Cayman islands based on a female specimen captured at Gonsteds, Grand Cayman on 21 April 1983 by Prosser.

Macrodiplax balteata (Hagen)
Another new record for the Cayman Islands, found only on Grand Cayman. The earliest capture we have noted is a female taken in April 1983 by Prosser at Barkers on the northwest coast. In September 1995, a male was caught by Askew at Botabano and a few days later, in October 1995, several individuals of both sexes were discovered on the upper beach at Conch Point. On the most recent visit to Grand Cayman, in February and March 1997, ***M. balteata*** was found to have become quite numerous, being seen at several sites in the south and east of the island, in addition to the original northwestern localities. This surge in records suggests that ***M. balteata*** might be a recent immigrant to Grand Cayman. Both sexes perch on prominent herbaceous plants beside pools of fresh or almost fresh water.

Pantala flavescens (Fabricius)
Recorded from Grand Cayman and Little Cayman by Fraser (1943), and from Cayman Brac by Askew (1994), this is a common dragonfly in the Caymen Islands (as well as in many other parts of the world). Large feeding

aggregations are often encountered flying at a height of 2-4 m., sometimes in the open but more usually near tree canopy.

Pantala hymenaea (Say)
this American species is usually much less common than its cosmopolitan congener, although Fraser (1943) records that the collections of the 1938 Oxford University Expedition included more specimens of ***P. hymenaea*** (8, from Grand Cayman and Little Cayman) than of ***P. flavescens*** (3). Subsequently, on Grand Cayman, a few were noted in August 1985, one at a street light in the evening and others among feeding aggregations of ***P. flavescens***.

Tramea abdominalis (Rambur)
Reported from Little Cayman in August 1975 (Askew, 1980), this record was later considered to refer to ***T. calverti*** (Askew, 1994). However, with the finding of both ***T. abdominalis*** and ***T. calverti*** in Grand Cayman by Prosser in 1983 and Askew in 1997, the Little Cayman record is now thought to be probably correct. It flies in mixed feeding aggregations with ***Pantala*** and other ***Tramea*** species. The frequencies of the three ***Tramea*** species caught (unselectively) in such aggregations on Grand Cayman in 1997 were: ***T. abdominalis*** 14; ***T. calverti*** 10; ***T. onusta*** 3.

Tramea calverti Muttkowski (= *Tramea cophysa* Hagen)
This species is usually more numerous than ***T. abdominalis*** on Grand Cayman. It was first reported by Fraser (1943), later by De Marmels and Racenis (1982) and Askew (1994). In the hand, ***T. calverti*** can be seen to differ ***from T. abdominalis*** in having pale stripes (more or less defined) on the sides of the thorax and more extensive black spots on the apical abdominal segments.

Tramea onusta (Hagen)
A new record for the Cayman Islands. A single male was caught by Askew at Botabano, Grand Cayman on 19.September 1995, and in February and March 1997 it was widespread on the island, twelve individuals being seen. In mixed feeding aggregations with other ***Tramea*** species, ***T. onusta*** is readily distinguishable by the large and characteristically-shaped hindwing basal mark.

DISCUSSION

Twenty-seven species of Odonata (5 Zygoptera, 22 Anisoptera) have now been recorded from the Cayman Islands (Table 1). All of these species have been found on Grand Cayman but many are not yet known from the two lesser Caymans. Faunistically, Cayman insects are most closely allied to those of Cuba and, to a slightly lesser extent, those of Jamaica and the southeastern United States (Askew, 1994). The Odonata are not exceptions. All Caymanian species of dragonflies are also found in Cuba. However, a number of species found in Cuba have not been reported from the Cayman islands. Some of these are presumably absent because of the lack of suitable habitat on Cayman (e.g. ***Progomphus*** species which require sandy-bottomed streams and lakes as larval habitat), but several others, particularly among the Libellulidae, could eventually expand the list of Cayman Odonata.

As it stands at present, the list of 27 Cayman species represents a substantial increase on the original list of 12 species which resulted from the 1938 Oxford University Expedition (Fraser, 1943). This expedition lasted only for a few months and Odonata were not the only animals to be studied by the two entomologists, Bernard Lewis and Gerald Thompson. Nevertheless, in February and March, 1997, Askew recorded 23 species on Grand Cayman in rather less than three weeks. This clearly indicates that there has been no diminution in species richness of Caymanian Odonata in the wake of many years intensive insecticidal spraying of mosquito breeding grounds. From the viewpoint of nature conservation one may hope that this faunal diversity reflects persistence of resident species rather than repeated replenishment by immigration.

Table I. Cayman Odonata and their occurrence on the three Cayman Islands, Cuba, Jamaica, and Florida. Data on distribution outside the Cayman Islands is from Needham & Westfall (1955), Paulson (1982), Dunkle (1989), and Westfall & May (1997)

	Grand Cayman	Cayman Brac	Little Cayman	Cuba	Jamaica	Florida
Lestes spumarius	X	X		X	X	X
Ischnura hastata	X			X	X	X
Ischnura ramburii	X			X	X	X
Leptobasis vacillans	X			X	X	
Nehalennia minuta	X			X	X	
Coryphaeschna viriditas	X			X	X	X
Anax amazili	X		X	X		X
Anax junius	X			X	X	X
Gynacantha nervosa	X			X	X	X
Triacanthagyna septima	X			X	X	
Micrathyria didyma	X			X	X	X
Brachymesia furcata	X	X	X	X	X	X
Brachymesia herbida	X	X		X	X	X
Orthemis "ferruginea"	X	X	X	X	X	X
Erythemis plebeja	X			X	X	X
Erythemis simplicicollis	X			X	X	X
Erythemis vesiculosa	X			X	X	X
Erythrodiplax berenice	X	X	X	X	X	X
Erythrodiplax umbrata	X	X	X	X	X	X
Erythrodiplax fervida	X			X	X	
Idiataphe cubensis	X			X	X	X
Macrodiplax balteata	X			X	X	X
Pantala flavescens	X	X	X	X	X	X
Pantala hymenaea	X		X	X	X	X
Tramea abdominalis	X		X	X	X	X
Tramea calverti	X			X	X	X
Tramea onusta	X			X		X

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TAXONOMIC AND POPULATION STUDIES OF BRITISH COLUMBIA *AESHNA* SPECIES

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ABSTRACT

Observations on aeshnid dragonflies and the examination of specimens collected during excursions through southern British Columbia (B.C.) from July to August 1995 led to the following results: (1) Mass emergences of dragonflies contribute considerably to the transportation of matter and energy from aquatic to terrestrial ecosystems. (2) Compared with the situation in northern central Europe (same latitude) the distribution and density of ***Aeshna juncea*** and ***A. subarctica*** in southern B. C. is impaired by larval competition by ***A. eremita, interrupta, palmata, umbrosa.*** (3) Species, mainly occurring at lower elevations (***A. interrupta, A. multicolor***) more clearly follow "Walker's Rule" than those less dependent on altitude or those preferring higher elevations. (4) The separation of ***A. septentrionalis*** and ***A. caerulea*** is confirmed by morphological characters, whereas the mere subspecific status of ***A. juncea americana*** within the ***A. juncea*** complex requires thorough investigation. A key using wing characters is presented for the determination of B. C. aeshnid species is presented. The examination of dragonfly wings discarded by birds has enabled the identification of the prey species.
Keywords: Aeshnidae, B. C., distribution, population density, larval growth, competition, "Walker's Rule", determination by wings, species distinctness.

INTRODUCTION

During a three week trip (July 16 - August 6, 1995) through southern British Columbia (including Vancouver Island, Okanagan Valley, Rocky Mountains near Golden, and the Clearwater area) the life and habitats of aeshnid dragonflies were studied and adults and exuviae were collected for comparative investigations of the holarctic ***Aeshna*** species groups. Because flight seasons of species vary from early to late summer and because of locally unfavorable weather conditions, I found only 11 of the 14 species of Aeshnidae occurring in southern B.C. I did not collect ***Aeshna septentrionalis, A. constricta,*** nor ***A. subarctica.*** I collected only exuviae of ***A. umbrosa.*** The failure to find the supposed holarctic species ***A. septentrionalis / caerulea***, ***juncea,*** and ***subarctica*** left me a little unsatisfied. Nevertheless, the answer to the still unresolved question of how many species there are in the ***caerulea*** and in the ***juncea*** groups, does not at all depend on fresh material from nearctic populations. The species are richly represented in the museum collections of Canada and the USA. The main hindrance to studies on the relationships between the North American and Eurasian odonate fauna is the deficiency of material from eastern Siberia (Belyshev 1973/1974). There are hardly any specimens available from the mainland east of the Lena River or from the Kamtschatka peninsula.

The nearctic dragonflies, particularly the aeshnids, have been studied intensively by numerous prominent odonatologists for more than 150 years. The regional dragonfly fauna of B. C. seems to be even better known than its equivalents in other parts of North America (Currie, 1905; Osburn, 1905; Walker, 1927; Whitehouse, 1941; Scudder *et al.*, 1976, Cannings & Stuart, 1977, Cannings & Cannings, 1994). Therefore, visiting B.C. for the first (and quite a short) time, I did not expect to make exciting discoveries or amazing observations. However, some of the findings presented here should be of interest.

MATERIAL COLLECTED

The material studied (174 adult aeshnids, 608 exuviae) was collected over 13 days. With a few exceptions the adults were captured in four areas (Table I): (1) Vancouver Island (Greater Victoria, Nanaimo, Hamilton Marsh near Qualicum Beach); (2) Okanagan region (valley between Okanagan Falls and Osoyoos, ponds on the Thompson Plateau west of Penticton and Okanagan Falls, "Venner Meadows" in the Okanagan Highlands east of Vaseux Lake); (3) upper Columbia River valley and headwaters of Kootenay River near Golden along the western slopes of the Rocky Mountains

(Redburn Creek in the Blueberry River valley; headwaters of Blackwater and Succour Creek with small lakes, fens and bogs; Susan lake, artificial ponds and lakes down the Columbia river between Brisco and Donald Station; Marion Lake and ponds near the headwaters of Kootenay River); (4) Clearwater area along the North Thompson River (beaver lake in the Dunn Lake valley 15 km south of Clearwater, small forest lake north east of Wavey Lake about 8 km north of Lac Des Roches, small lakes and bogs on the northern slopes of Mt. Grizzly northwest of Clearwater, Graffunder Lakes 12 km east of Vavenby). A few specimens were caught while traveling between these areas (included in Table I in the column "total number..."): three ***A. palmata*** (Silver Lake near Hope); two ***A. eremita***, one ***A. interrupta*** (near Jasper, Alberta); two ***A. interrupta*** (near Kamloops) and two ***A. palmata*** (Coquihalla Creek near Coquihalla Lake northeast of Hope).

During the journey some aeshnid exuviae were casually collected in a number of fens, ponds, and small lakes, while others were found during thorough searches, mostly on cool or rainy days (Table II). Exuviae are useful in answering questions of population ecology (density, competition) and distribution (presence or absence of species in space and time). Statistically representative samples of exuviae can be used to calculate sex ratios in populations and species or to determine differences in final growth measurements between colonies. The value of exuviae collections should not be underestimated. When dealing with rare or endangered species or species colonies, exuviae may serve as the only but fully acceptable evidence of their occurrence.

FAUNISTICS AND ECOLOGY

From the faunistic point of view the darners collected during this journey do not contribute new information to the known distribution pattern of aeshnids in southern B. C. (Cannings & Stuart, 1977; Cannings & Cannings, 1994). The same is true for the exuviae, with one exception; exuviae of ***A. tuberculifera*** were found at a forest lake and a beaver pond along the western slopes of the Rocky Mountains near Golden: the exuviae of one male and one female at Marion Lake (headwaters of Kootenay River), and one male and five female exuviae in the Blueberry River valley (Redburn Creek). These records expand the range of this species in the interior of southern B. C. In both water bodies ***A. tuberculifera*** coexists with larvae of ***A. eremita, A. interrupta, A. palmata, A. umbrosa*** and, at least in the beaver pond (Redburn Creek), with ***A. canadensis*** (as it does in Hamilton Marsh on Vancouver Island) (Table II).

The series of exuviae from a lake near Castledale in the Columbia River valley deserves some attention, not only because of the large number of specimens (257), but mainly because of the small size of the area where they were collected, which was only 6 x 1.5 m along the northeastern border of the lake. At this place, the broad belt of *Scirpus* surrounding the lake, which was here and there intermingled with cat-tail (*Typha*), was narrow and sparse. ***Aeshna*** larvae ready for emergence usually avoid thickets of emergent vegetation and concentrate where stems are less dense. Because favorable places for emerging darners were numerous along the shore of this eutrophic lake, which was partly covered with water lilies, this water body probably produced thousands of aeshnids. Mass emergences of dragonflies as described above are regularly seen throughout the Holarctic in small garden ponds as well as in lakes of the Mongolian steppe (Peters 1985). Thus the contribution of dragonflies to the transportation of matter and energy from aquatic into terrestrial ecosystems may play an important role in the ecosystem's economy and may even be more weighty than that of other groups of amphibious animals.

It was inevitable for European eyes to compare the Cordilleran aeshnid fauna to its counterpart in the Western palearctic. In B. C. and Europe between the 49th and 55th degree of latitude the numbers of species are nearly equal (13 and 11) and the composition of species is similar. ***Aeshna*** species prevail (12 and 8, including "***Anaciaeschna" isoceles***) and ***Anax*** is represented by 1 and 2 species, respectively. The only difference of some (historical) importance is the lack of Brachytronines in B. C. which is compensated by the presence of ***Tanypteryx*** (Petaluridae).

The climatic conditions of the interior plateaus of B. C. are comparable to those of eastern Europe, those of the Rocky Mountains (between 49° and 52°N) with those of the Alps, and those of the Lower Mainland and eastern parts of Vancouver Island with those of western central Europe. On both continents the distribution of darners is mainly (but not exclusively) determined by climatic factors such as temperature, insolation, and moisture during summer. The altitudinal gradation of these factors influences the distribution patterns of species according to their preferences. For instance, in places higher than 800 m. ***A. interrupta*** is more and more replaced by ***A. palmata.*** A comparable situation does not exist in central Europe. Moisture (rain, cloudiness, mist) as a major factor reducing summer heat seems to be responsible for the fact that the boreal species ***A. juncea, A. sitchensis***, and ***A. subarctica*** can be found near sea-level on Vancouver Island while they are missing in the drier interior parts of southern B. C. However, there is a great difference in central Europe: ***A. juncea*** has many lowland colonies in shallow boggy forest fens as well as in artificial fish-ponds (comparable to some extent with Canadian beaver ponds) in Saxonia (Germany) and Czech Republic, and is the dominant species there. ***A. subarctica*** occurs in almost all remaining lowland *Sphagnum* bogs and ponds between moraine hills a little further north (52° - 56° N), and is accompanied by small colonies of ***A. juncea*** (Peters, 1992). Even ***A. caerulea*** has been reported from lowland bogs in Belorus (Ander, 1950) and southern Sweden (Peters, unpubl.). Therefore, I was surprised not to find these three species in favorable habitats in the Clearwater region. I had the impression that the habitats around Golden suitable for larvae of ***A. juncea*** were only partly colonized by this species. At higher altitudes near Clearwater (small boggy sedge-bordered lakes to the northeast of Lac de Roches at 1100 - 1200 m or east of Vavenby at 1600 - 1700 m) ***A. eremita*** and ***palmata*** were the only species present. At the shallow boggy pools with floating *Sphagnum* near the Grizzly Lakes (1500 - 1600 m) northwest of Clearwater (Grizzly Mountain), which appeared to be good places for ***A. subarctica***, again, only single exuviae of ***A. eremita*** and a few of ***A. palmata*** were found.

Without doubt, the climatic and microclimatic conditions are the main factors responsible for distribution patterns of the boreal darner species near the southern boundaries of their ranges. However, when regarding the absence of ***Aeshna juncea*** and ***A. subarctica*** from suitable places, some attention should be paid to the interspecific competition. In B. C. specimens of ***A. juncea*** are markedly smaller than those in the western palearctic. They are even smaller than ***A. palmata*** and, at lower elevations, may suffer from competition with the large larvae of ***A. eremita.*** This situation is different from that in central and southern parts of northern Europe (Russia, southern Sweden), where specimens of coexisting colonies of darners in peat bogs and boggy forest lakes are more or less of the same size (***A. juncea, A. subarctica, A. grandis*** and ***A. cyanea***). Only in eutrophic ponds and lakes where ***A. juncea*** and ***A. subarctica*** do not occur, do the larvae of ***A. grandis*** and ***A. cyanea*** reach the size of ***A. eremita*** larvae (Peters, 1988).

There is a further argument for increased competition between darner colonies in the mountains of B. C. compared with the situation in Europe: Above 1000 m in the Alps and above 700 - 800 m in central Sweden ***A. juncea*** and ***A. subarctica*** (occasionally accompanied by ***A. caerulea***) are the only ***Aeshna*** species present, whereas in southern B. C. the small-sized ***A. juncea*** has to compete with ***A. eremita, A. palmata, A. umbrosa***, and in some places even with ***A. interrupta*** and ***A. tuberculifera.*** To a lesser degree the same is true for ***A. subarctica.*** Thus, the observed patchiness of the distribution of ***A. juncea*** around Golden and Clearwater may partly be the result of competition between the larval populations involved. Further north the physical conditions change in favor of ***A. juncea***, although almost all species mentioned above are still present. ***A. juncea*** has been reported from the Yukon Territory as "the commonest ***Aeshna***, found in virtually every sedge pothole and marsh in the forested regions" (S. G. Cannings *et al.,* 1991).

SIZE AND PROPORTIONS OF SPECIES

All captured darners were measured for body length (l), length of abdomen without appendages (abd) and wingspan (ws). Mature specimens were weighed after they were held alive overnight in envelopes, eliminating material in the gut. Two body proportions were calculated: relative length of abdomen = abd/l x 100; relative wingspan = ws/l. As a measure of slenderness the ratio between weight (w) and body length (l) was used (w/l calculated in g per 1 mm of length). Determining the size of exuviae is time-consuming because of the preparations necessary to restore the natural position and extension of the abdominal segments. For comparison among species the width of the head capsule, usually well preserved, serves as a relative measure for the size of the larvae. The lengths of hindwing cases and the labium may also be used. Data sets of measurements and body proportions contain valuable information about species and group specific characters, not only for systematic purposes but also for ecological studies.

E. M. Walker (1912) showed that the slenderness of the dragonfly body is correlated with the mean summer temperature. In regions with cooler summers the specimens will have a stouter appearance because of the measurable shortened and widened third abdominal segment (see Plate 1 of his monograph). It remains to be investigated whether or not "Walker's Rule" is an example of a more general ecological generalization called "Bergmann's Rule" (Mayr, 1942). In eutrophic ponds the larvae of "generalist species" grow larger than in mesotrophic or oligotrophic waters, as observed for ***Aeshna grandis*** and ***A. cyanea*** in Europe, probably because of presence of more food (Peters, 1987, 1988).

Table III contains information about size and body proportions of adults of several ***Aeshna*** species, which might be useful in further investigations:

1. ***A. multicolor*** has the relatively shortest abdomen of all species under comparison. It is not known if this character is species specific or is an attribute of the ***Schizuraeschna*** group as a whole.

2. As a rule of thumb, the w/l-ratio increases with body length. The ***A. interrupta*** males from the mountain regions around Golden and Clearwater are an exception. They are remarkably heavier, when compared with the ***A. interrupta*** males from Vancouver Island and the Okanagan, i. e., they are more stoutly built, thus confirming the findings of Walker (1912), stated above. The females also follow this rule.

If larger series of specimens were available, other species widely distributed in southern B. C. should show the same results. Some data - not included in the table - can be presented for ***A. canadensis***, ***A. multicolor***, and ***A. tuberculifera***: In the Dunn Lake valley south of Clearwater (small beaver lake at 800 m) males of ***A. canadensis*** are slightly smaller (67.6 - 69.6 mm) than at Hamilton Marsh (69.3 - 70.8 mm), but at the beaver lake two very large males (72.2 mm) were netted. On average, the four exuviae from Hamilton Marsh are larger (mean length of labium 6.98 mm) than the five specimens from Golden (Redburn Cr.) and the Dunn Lake valley (6.79 mm). However, one Redburn exuvia was larger than the largest one from Hamilton Marsh. If mean size differences exist between lowland (coastal) and highland populations, a broad overlap within the ranges of the parameters is to be expected. With the examination of additional material, ***A. tuberculifera*** will likely show a similar situation: larger specimens will be relatively more numerous along the slopes of the Rocky Mountains than on Vancouver Island, where on average the exuviae have a somewhat smaller labium (8.7 compared to 8.9 mm).

The five ***A. multicolor*** males from the Golden and Clearwater area are similar in size to the smaller specimens of the series caught at Vancouver Island, but according to their weight they belong to the nine heaviest of all netted adult males. Their relative weight (0.0090-0.0096 g/mm) is reached only by two of the 20 Vancouver Island males. Thus, this species represents another example of the "Walker's Rule" mentioned above.

A. palmata does not seem to follow that rule: both smaller and heavier specimens were found at every collecting site.

Thus, populations of species that prefer lower elevations in southern B. C. (***A. interrupta, A. multicolor***) more clearly follow "Walker's Rule" than those less dependent on altitude (***A. canadensis, A. tuberculifera***) or those preferring higher elevations (***A. palmata***).

IDENTIFICATION OF SPECIES BY WING CHARACTERS

If the clear and well-illustrated keys for darners in the handbook of B. C. dragonflies (Cannings & Stuart, 1977) are used , the identification of adults or larvae (exuviae) should be straight forward. Occasional doubts about the validity of the distinguishing characters, for instance in case of small ***A. eremita*** or exceedingly large ***A. canadensis*** males, can be eliminated by comparing their secondary copulatory organs with the adequate drawings in the classical monograph by Walker (1912).

However, in dealing with the remnants of dragonflies eaten by birds, I was faced with the problem of determining the aeshnids by their wings alone - a well-known exercise to paleontologists when dealing with fossil remnants of Odonata. In principle, it should be possible to determine every species of darner by its venational characters, but for comparison and calculations of variability a complete collection (a series of males and females of all local species) should be at hand.

The wings of Aeshnidae are easily recognized by their elongated discoidal triangles. The females of all aeshnid species in the Holarctic possess relatively longer pterostigmata and relatively broader hind wings compared with the wings of the respective males, which are characterized by their well-marked hindwing anal triangle (excluding ***Anax***). Thus, calculations of the "Pt-ratio" (length of pterostigma, as a percentage of the distance between nodus and proximal point of Pt along wing border) and, in case of ***Anax***, the "wing-ratio" (maximum width of hindwing as a percentage of wing length) are necessary for sex determination. Some experience is needed to separate wings of mature specimens from those of freshly emerged ones.

In B. C. separated wings of ***Anax junius*** are easily recognized by their very long pterostigmata, the bulging of vein R3 under Pt, the divergence of the veins A2 and A1, and the unforked R3-vein (fig. 1). All Canadian ***Aeshna*** species have shorter Pt, no R2-bulging, A2 being parallel to A1 (the anal loop is parallel-sided), and a well-marked IR3-fork (fig. 2-12).

As already described by Walker (1912), ***A. californica*** and ***A. multicolor*** are distinguished from all other western Canadian species by the symmetry of the IR3-fork of all wings (fig. 2,3). The alternative character state is a more abruptly arched anterior branch (fig. 6).

The wings of ***A. sitchensis*** and ***A. septentrionalis*** differ from others in the long row of double cells between the veins R3 and IR3 above the IR3-fork (fig. 4,5). In wings of male ***A. sitchensis*** Pt is markedly longer than in ***A. septentrionalis*** males. If the same difference occurs in females (I have not seen ***sitchensis*** females), it should be possible to separate wings of female ***septentrionalis*** from wings of male ***sitchensis*** exclusively by "Pt-ratio".

Double cells in the mentioned position (doubtless a plesiomorphic pattern) are found in the wings of other ***Aeshna*** species. The percentage of specimens possessing double cells and the mean number of these cells per wing is highest in ***A. eremita*** (about 70 % of specimens; 2.6 double cells in males, 3.5 in females).

For the determination of the majority of the ***Aeshna*** species in B. C. by wings alone the position of IR3-fork and the starting point of vein IR2 in relation to Pt should be noted. Additionally, the "IR3-fork-ratio" should be used; this is the distance between nodus and IR3-fork given as a percentage of the distance between nodus and proximal point of Pt at the wing border (fig. 11,12).

As seen in the key, I was unable to distinguish between the wings of ***A. constricta*** and ***A. palmata.*** Hopefully, this problem will be solved when more material is available. The characters "3-celled anal triangle" and "conspicuously short Pt" had to be omitted from the key, because in ***A. constricta, A. palmata,*** and ***A. umbrosa*** only the males can be distinguished by these characters from the remaining species having an asymmetrical IR3-fork. All measurements and ratios used in the key were calculated from hindwing measurements.

KEY FOR DETERMINATION OF B. C. AESHNIDAE USING WING CHARACTERS

1 R3 markedly curved (bulged) towards R2 beneath distal part of Pt; IR3 not really forked (fig. 1) .... ***Anax junius***

1' R3 evenly bent; IR3 distinctly forked (fig. 2-12) 2

2 IR3-fork symmetrically branched (fig. 2,3) 3

2' IR3-fork asymmetrically branched (fig. 4-12) 4

3 Hindwing shorter than 40 mm; IR3-fork situated 1-1 ½ cells proximal to Pt and with 11-14 cells below its anterior branch (fig. 2) ..... ***A. californica***

3' Hindwing longer than 40 mm; IR3-fork situated 2-3 cells proximal to Pt, and with 15-18 cells along its anterior branch (fig. 3) .... ***A. multicolor***

4 With a long row of double cells (fig. 4,5) between R3 and IR3 before and beyond the IR3-fork; hindwing shorter than 42 mm 5

4' No continuous row of more than 5 double cells above the IR3-fork (exceptionally more than 5 double cells in ***A. eremita***, which has a hindwing longer than 45 mm; see fig. 11) 6

5 Pt long (3.6-4.2 mm in males, with "Pt-ratio" more than 25 %; female conditions unknown; fig. 4) .... ***A. sitchensis***

5' Pt relatively short ("Pt-ratio" 22-24 % in males, in females 27-30 %; fig. 5) .... ***A. septentrionalis***

6 IR3-fork near the level of the proximal end of Pt (fig. 6,7) 7

6' IR3-fork situated 2-3 cells before Pt (fig. 8-10, 12) 9

7 Hindwing usually longer than 44 mm ....***A. eremita***

7' Hindwing usually shorter than 44 mm 8

8 Proximal oblique connecting vein between IR3 and Rspl relatively short, and at an angle of about 60° (fig. 6); hindwing "Pt-ratio" in males 22-24 %, in females 21-28 % .... ***A. juncea***
8' The first oblique connecting vein between IR3 and Rspl relatively longer and at an angle of about 45° (fig. 7); hindwing "Pt ratio" in males 19-22 %, in females 21-28 % (as in *A. juncea*)
.... ***A. interrupta***
9 Vein IR2 arising at a point before the middle of, or at the middle of, the Pt 10
9' Vein IR2 arising at a point beyond the middle of the Pt (fig. 8) ....***A. constricta, A. palmata***
10 IR3-fork situated 1-1½ cells before the anterior point of Pt (fig. 9) .... ***A. subarctica***
10' IR3-fork situated at 2-3 cells before the anterior point of Pt 11
11 IR2 begins mostly irregularly with double cells (1-3); Pt of male wings hardly longer than 3 mm (fig. 10) .... ***A. umbrosa***
11' IR2 starts as a straight (regular) vein (fig. 12) 12
12 Distance Nodus - Pt more than 19.0 mm
.... ***A. tuberculifera***
12' Distance Nodus - Pt less than 19.0 mm (16.0-18.6 mm) 13
13 "IR3-fork ratio" with single exceptions more than 86 % (86-91 % in males, 88-92 % in females) (fig. 11) .... ***A. eremita***
13' "IR3-fork ratio" less than 85 % (77-83 % in males, 80-85 % in females) (fig. 12)
.... ***A. canadensis***

This first draft of a wing-based key and the problems concerning the distinction of ***A. constricta*** and ***A. palmata*** still include some uncertainties. Further characters, measurements, and ratios substantiated by examination of representative samples of both sexes of all species should be incorporated. If the species' distribution and local ecological preferences are known at a given area usually some species can be excluded with a considerable degree of certainty. For instance, in southern B. C. ***A. sitchensis*** and ***A. septentrionalis*** will rarely, if at all, be found together in a particular place.

The key presented above was developed to determine the contents of two small heaps of wings, one found on the trunk of a fallen tree at Blinkhorn Lake in Metchosin (southern tip of Vancouver Island), and the other one at the beaver lake in the Dunn Lake valley 15 km south of Clearwater. The first sample (July 15) contained 37 ***Aeshna*** wings (and all four of one ***Libellula forensis*** specimen). ***A. californica*** was represented by 2 right and 2 left fore wings, and 2 right and 1 left hindwing (2 specimens) and ***A. multicolor*** by 5 right and 8 left fore wings and 7 right and 10 left hind wings (10 specimens).

The beaver lake sample (August 2; 17 wings) comprised 2 right and 2 left hind wings of ***A. eremita*** (2 specimens) as well as 3 right and 3 left fore wings and 3 right and 4 left hind wings of ***A. canadensis*** (4 specimens). To my surprise both piles exclusively consisted of female wings, and all but one pair of hind wings (***A. eremita***) were from fully mature adults. This observation can be explained only by assuming that the victims were egg-depositing females. There must be songbird species specialized in catching dragonflies just during these dangerous moments of their life-cycle. R. A. Cannings informed me that probably the Song Sparrow (*Melospiza melodia*) and perhaps the Red-winged Blackbird (*Agelaius phoeniceus*) may be the predators in question. As far as I know, no similar observations have been made in Europe, where occasionally considerable numbers of newly emerged dragonflies are killed by songbirds (*Acrocephalus arundinaceus, Motacilla alba, Turdus merula, Passer domesticus* and others) in order to feed their nestlings.

SPECIES DISTINCTNESS AND VICARIANCE

Since the publication of Walker's excellent monograph (1912) no serious doubts about the distinctness of the North American darners have arisen - with one exception: ***Aeshna septentrionalis.*** In 1958 E. M. Walker returned to the position of Calvert (1905), pointing out that ***septentrionalis*** should no longer be treated as a mere subspecies of ***A. caerulea***, but as a full species: "Undoubtedly their affinities are extremely close, but the differences between them, though slight, appear to be constant." The majority of the odonatologists followed this decision (Needham & Westfall, 1955; Scudder, Cannings & Stuart, 1976; Cannings & Stuart, 1977; Davies & Tobin, 1985 and others). The two species differ only in the form of the first thoracic stripe, but also in the shape of the anal appendages in both sexes (Walker, 1912, 1958; Valle, 1950). The male superior appendages are "much broader in ***septentrionalis*** than in ***caerulea***" (Walker 1958) and - as should be added here - the appendages of the former bear no dorsal spines and no ventral projection (fig. 13). A specimen caught by R. A. Cannings in the Magadan region of eastern Siberia, has these traits in common with western palearctic ***caerulea*** males.

It is still unknown whether the similar species-specific differences between ***septentrionalis*** and ***caerulea*** also occur within the two other holarctic ***Aeshna*** species, ***A. juncea*** and ***A. subarctica. A. juncea*** seems to be a highly polymorphic ensemble of distinctive allopatric entities (ornithologists tentatively would name it a "superspecies"); eight subspecies have already been described mainly based on differences in color pattern. However, structural characters and body proportions will have to be included in a thorough analysis of the geographical variation and distribution pattern (vicariance) of the ***juncea*** complex. The results should help answer the question whether or not ***A. juncea americana*** - along with some other subspecies - can be interpreted as a full species. In the case of ***A. subarctica***, currently subdivided into a nearctic (***subarctica***) and a palearctic subspecies (***elisabethae***), its taxonomic status has as yet not been questioned in the literature.

The distinctness of species within the holarctic ***Aeshna*** species complexes is not a question confined to ***Aeshna.*** Very much remains to be learned about the morphological variability of species of other genera of dragonflies (***Lestes, Enallagma, Somatochlora, Libellula, Sympetrum*** etc.) as well as of other insect taxa in order to substantiate ideas about the history of Beringia. If the supposed land bridge between Siberia and Alaska was unsuitable for penetration of heterothermic animals from the beginning of the Miocene to the Pleistocene due to the proposed proximity of the North Pole during that time span (Wegener's theory), then holarctic distribution of species has been limited to the times before the Neogene, the Pleistocene interglacials, and to the early Holocene (Matthews, 1979, Noonan, 1988). On the other hand, at least up to the Oligocene, faunal exchange between the Nearctic and Palearctic should have been possible via Labrador, Greenland, Iceland and Scandinavia (Noonan, 1988).

Only by analyzing the questions of species distinctness and phylogenetic relationships of the apparently trans-holarctic dragonfly species can serious arguments for a profound vicariance of the holarctic fauna be found.

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Table I
Aeshnids netted in southern B. C. in July/August, 1995

	Vancouver Island Jul13-16	Okanagan area Jul 20-22	Rocky Mountains near Golden Jul 24-26	Clearwater area Jul 30-Aug 3	total males/ females
Anax junius	1				1/0
Aeshna californica	3				3/0
A. canadensis	10			14	21/3
A. eremita			1	21	22/2
A. interrupta	2	8	19	22	35/19
A. juncea			4		3/1
A. multicolor	26	1	1	4	25/7
A. palmata	1	9	1	13	26/3
A. sitchensis	1		1		2/0
A. tuberculifera	1				0/1

Table II
Samples of ***Aeshna*** exuviae from different places in southern B. C.

	numbers of specimens								
	can.	***ere.***	***int.***	***jun.***	***mul.***	***pal.***	***tub.***	***umb.***	total
Vancouver Island: Hamilton Marsh	4				4		15		23
Golden 13 km N: Typha pond along Columbia River		39	7			1			47
Castledale, 2 km NW: artificial Columbia River valley lake		74	257			9			340
Blaeberry-River: Beaver pond and creek near Redburn creek	4	9	1			3	6	5	28
NW of Donald Station: Aid Lake		2						14	16
Kootenay River headwaters: Marion Lake		23	13			11	2	2	51
Beaverfoot River valley near Kicking Horse River: forest pond and beaver lake		20		11		4			35
Clearwater 15 km S, Dunn Lake valley: beaver lake	1	13	1						15

Table III
Size and body proportions of adults of several ***Aeshna*** species in southern B. C.

species	sex	n	l	w	abd/l	ws/l	w/l
californica	m	3	62.7	0.38	67.3	1.29	0.0060
multicolor	m	25	68.3	0.56	64.6	1.39	0.0083
multicolor	f	7(6)	68.3	0.62	63.3	1.40	0.0092
canadensis	m	21	69.5	0.55	68.5	1.32	0.0079
canadensis	f	3	68.2	0.67	69.2	1.35	0.0098
eremita	m	22	77.1	0.78	69.3	1.30	0.0100
eremita	f	2(1)	76.0	0.84	68.0	1.36	0.0115
interrupta (Okan)	m	8	69.7	0.54	67.7	1.34	0.0076
interrupta (Mt)	m	25	69.4	0.61			0.0090
interrupta (Okan)	f	2	69.2	0.58	67.9	1.40	0.0088
interrupta (Mt)	f	19(8)	66.3	0.67			0.0100
tuberculifera	f	1	78.2	-	68.4	1.33	-
juncea	m	3	68.2	0.61	68.3	1.31	0.0089
juncea	f	1	67.8	-	68.9	1.28	-
palmata	m	25	70.8	0.61	68.6	1.29	0.0085
palmata	f	3(2)	68.2	0.76	67.8	1.31	0.0110
sitchensis	m	2(1)	62.8	-	68.4	1.34	

n gives the number of specimens, in parentheses the number of mature ones; all data calculated from $n \geq 6$ are statistical means, data from 2 to 3 specimens are average ones. Okan contains 1 male and 1 female of ***A. interrupta*** from Vancouver Island and 7 males and 1 female from Okanagan. Mt comprises the ***interrupta*** specimens from the Golden and Clearwater region. l = length in mm, w = weight in g, abd/l = length of abdomen in percent of body length, ws/l = ratio of wingspan to body length, w/l = weight in g per mm of body length

following page:
Figs. 1-12: Right hindwings of ***Anax junius*** (fig. 1) and eleven ***Aeshna*** species from specimens collected in B. C.. Grey triangles indicate characters used in the key. Fig. 13: Male superior appendix of ***A. caerulea*** (above) and ***A. septentrionalis*** (below) in lateral view. (computer graphic by P. Schönefeld)

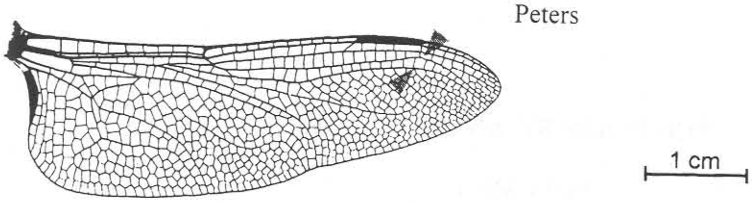

fig. 1 junius ♀

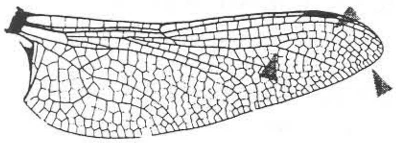

fig. 2 californica ♂

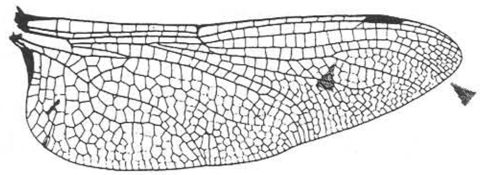

fig. 3 multicolor ♀

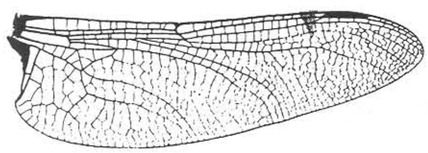

fig. 4 sitchensis ♂

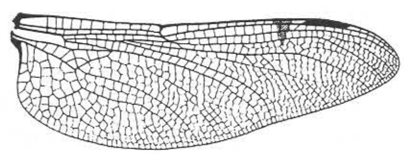

fig. 5 septentrionalis ♀

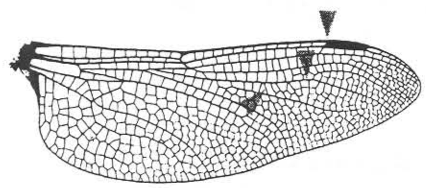

fig. 6 juncea ♀

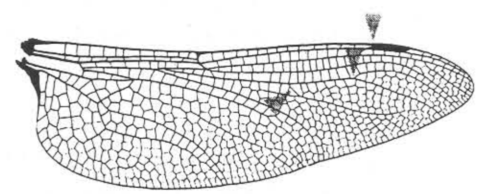

fig. 7 interrupta ♀

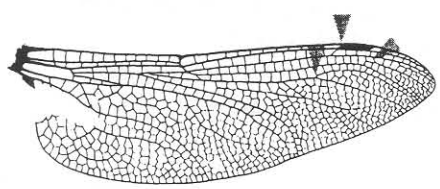

fig. 8 palmata ♀

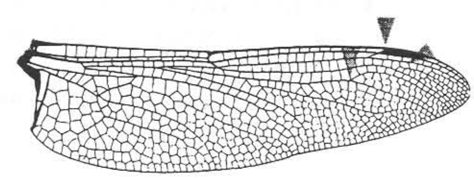

fig. 9 subarctica ♂

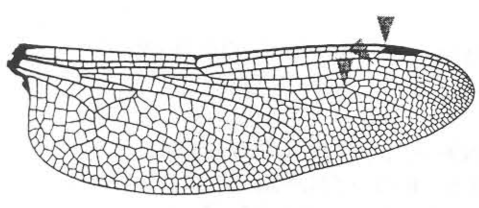

fig. 10 umbrosa ♀

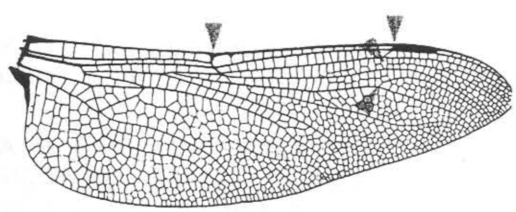

fig. 11 eremita ♀

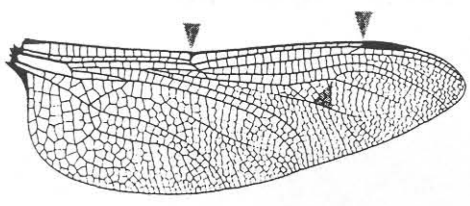

fig. 12 canadensis ♀

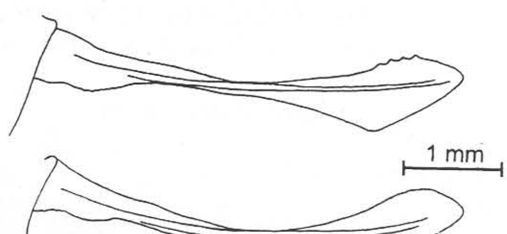

fig. 13

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