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Milen Marinov

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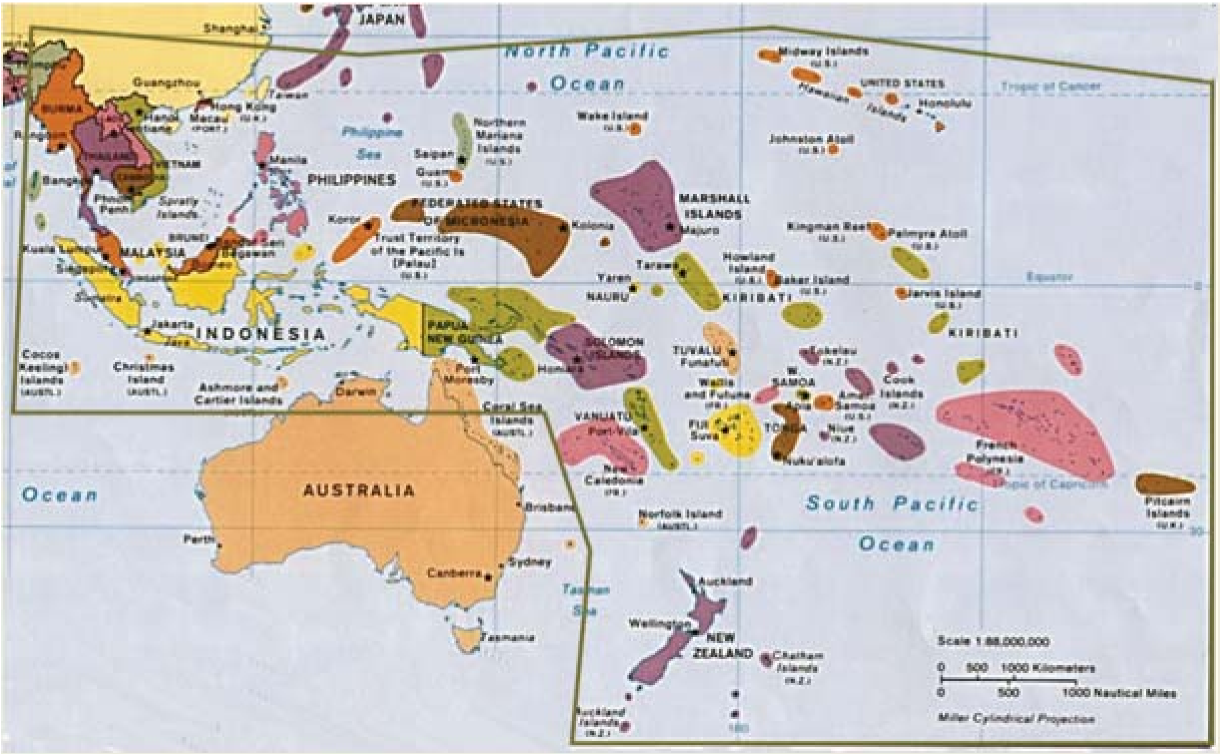
Pacific Islands comprise of Micronesian, Melanesian and Polynesian Islands.



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The seven “oddities” of Pacific Odonata biogeography

Milen Marinov

Plant Health & Environment Laboratory, Investigation and Diagnostic Centres and Response,
Ministry for Primary Industries, 231 Morrin Rd, Auckland, New Zealand.
E-mail: milen.marinov@mpi.govt.nz

Abstract

The existing literature on the Odonata inhabiting the three large divisions of the Pacific Ocean (Micronesia, Melanesia, Polynesia) is revised taking into consideration earlier discussions on the species origin, historical faunistic records, various palaeogeographical models proposed for the area, general data on the biology and ecology of this insect order. Special emphasis is paid on the incomplete data set for the region and inconsistency of the exploration of this vast area. The taxonomy and fauna of the Pacific Odonata is far from complete which makes it very difficult to provide any plausible hypothesis on the biogeographical pattern that we observe today.

The widely accepted view of long distance dispersal from a centre of origin as the only possible means for species to occupy remote oceanic island archipelagos is critically reviewed. There are seven phenomena in the current Odonata distribution that cannot be explained only by random gene transfer mediated by wind dispersal. Those are called “oddities”, however, they are believed to be regularities of past geological events and modern day human associated activities within the Pacific. The rationale for each of them is explained in details and illustrated with distribution maps following the current taxonomy of the group.

A new approach is suggested to tackle the question of the origin of the Pacific Odonata by relating the higher taxa distribution to the geological events and palaeontology of the families. It is not intended to be a new hypothesis yet before more systematic studies of the taxonomy and fauna of the group. Therefore, it is believed that the new method suggested here will increase the attention of the scientific community and will boost studies on this insect order within the Pacific Ocean. Discussion on its applicability is provided with attention to details that are difficult to be explained with the Pacific Odonata palaeontology as we know it for the moment.

Key words: Odonata, Pacific Ocean, biogeography, plate tectonic, expanding earth, Micronesia, Melanesia, Polynesia

Introduction

MacArthur & Wilson (1967) proposed a Theory of the Island Biogeography in which an island biota is a function of the immigration rate from a population on a mainland and the extinction rate. Species richness is negatively correlated with the distance from the source (MacArthur & Wilson 1963). Individuals or groups of dispersing organisms struggle to overcome large oceanic distances, therefore remote islands are characterised with an impoverished fauna and increased endemism (Gillespie 2007).

The invent of molecular techniques and the rapid development of molecular clocks (Zuckerkandl & Pauling 1965) provided an invaluable tool for building evolutionary timescales (Kumar 2005). Clock studies have contributed to dating divergence time (Jordan et al. 2003), with phylogenies calibrated using known fossil age (Benton & Donoghue 2007) (usually based on the age of the strata where the fossils were deposited; Ho & Phillips 2009). Volcanic islands that postdated the opening of the oceans and are situated hundreds of kilometres from the continents rely on the dispersal power of the organisms to be colonised (Smith 2009).

Damselflies and dragonflies (Insecta: Odonata), hereafter dragonflies or odonates, have proved suitable for a wide range of studies (Corbet & Brooks 2008). They have a perfect structure for long distance flight (Corbet 1999). Once air-borne they are capable of great acceleration, the maximum flight speed being 10-15 m/s (Suhling et al. 2015). Movements across continental land or sea straights have been reported for a number of species, but most migratory taxa are known in the superfamily Libelluloidea (Sánchez-Herrera & Ware 2012). Williams (2009) reports on what is believed to be the longest migration route in the insect world in *Pantala flavescens* (Fabricius, 1798). This species appears to be a regular visitor over the Maldives from India on the way to Africa. *P. flavescens* is a circumtropical species well known for its transoceanic invasions into temperate regions (Sakagami et al. 1974), with individuals discovered in extreme habitats such as Himalayas (Jackson 1955) or localities such as Easter Island (Dumont & Verschuren 1991). Molecular investigations indicate constant gene exchange through East Asia (Hayashi et al. 2003). However, another molecular study (Samways & Osborn 1998) established that there were morphological and behavioural differences between *P. flavescens* populations on the Easter Island and continental Africa.

Dispersal supported by air circulations is used mainly to explain the distribution of *P. flavescens* and other odonates occupying vast areas. Rowe (2004) divides dragonflies into two groups: a widely dispersed fauna capable of considerable trans-oceanic movements (Zygoptera: *Agriocnemis* Selys, 1877; *Ischnura aurora* (Brauer, 1865); Anisoptera: *Anax* Leach, 1815; *Anaciaeschna* Selys, 1878; *Gynacantha* Rambur, 1842; *Hemicordulia* Selys, 1870; *Diplacodes* Kirby, 1889; *Macrodiplax* Brauer, 1868; *Orthetrum* Newman, 1833; *P. flavescens*, *Rhyothemis* Hagen, 1867; *Tholymis* Hagen, 1867; *Tramea* Hagen, 1861) and local endemics (not specified). All Anisoptera are exceptional fliers, but the very delicate *Agriocnemis* and *I. aurora* are minute species that are unlikely to overcome large ocean barriers by their flight abilities only.

While *P. flavescens* is variously believed to reached Easter Island by its own power (Kevan 1965; Samways & Osborn 1998) or on human boats (Dumont & Verschuren 1991), *I. aurora* is always regarded as an air-borne dispersalist that is blown by the wind and thus spread across the entire Pacific (Armstrong 1958, 1973; Belyshev 1969; Donnelly 2005; Fraser 1925, 1927; Lieftinck 1962; Tillyard 1924). Rowe (1978) observed adult male *I. aurora* mating with teneral females and suggested that perhaps they can disperse, apparently without feeding for several days, to form a new colony. He proposed parthenogenesis as a possible way for this species to colonise new islands. Endersby (2002) suggested that this idea explains the populations on the Norfolk Island.

The contemporary Odonata species of the three large divisions of the Pacific – Micronesia, Melanesia and Polynesia – are believed to be descendants of immigrants from SE Asia-New Guinea-Australia region. Below is a short summary of the main literature on the biogeography of the Pacific Odonata.

For Micronesia all authors are in favour of SE Asian (Indonesia included) influence. Lieftinck (1962) did not specify the ultimate origin of the biota, but commented on the migratory habits of odonates and their ability to cover great distances across seas, either actively or passively. Belyshev (1969) established additional influence from Melanesia and subholarctica, but no American elements. Buden & Paulson (2007) proposed an Indo-Australian origin for six of the breeding odonates on Yap, and Buden (2008) reported that all species from Nauru are widespread across the Pacific.

For Melanesian odonates, wind dispersal is also the preferred scenario, with researchers suggesting various centres of origin that are sometime vague. Davies (2002) speaks about relations of New Caledonian species to northern and easterly sources without specifying sources other than east Australia and Papua New Guinea which are west and north-west to New Caledonia. Lieftinck (1975) also favoured aerial arrival of the New Caledonia Odonata at irregular intervals during the Plio-Pleistocene. Local endemic genera *Synthemis* Selys, 1870 and *Eoargiolestes* Kalkman & Theischinger, 2013 are believed to be earlier colonisers (Vick & Davies 1988), while *Ischnura* Charpentier, 1840 and *Oreaeschna* Lieftinck, 1937 are later arrivals, presumably from east Australia and/or Papua New Guinea (Vick & Davies 1990).

For the Solomon Islands Lieftinck (1949) supported a strong influence from Australia and Papua New Guinea. He was inclined to accept aerial dispersal from Australia even for such a weak flyer as *Eusynthemis* Förster, 1903, while for Libellulidae, like *Agrionoptera insignis allogenes* Tillyard, 1908 and *Rhyothemis phyllis chloe* Kirby, 1894, he suggested a direct arrival from Australia. Species on smaller islands such as Rennell Island originated from larger islands within the archipelago, possibly Makira and/or Guadalcanal (Lieftinck 1968).

Vanuatu has received little attention from biogeographers. Belyshev & Haritonov (1983) argued that in Vanuatu the Asian influence weakens and is replaced by the strong flow of immigrants from Australia, either directly from the continent or via New Guinea.

Polynesia encompasses a very wide area sprinkled with small island archipelagos, with the Fiji Islands being the largest group in this biogeographic province (Belyshev & Haritonov 1983). Donnelly (1984) commented on the close relation between Fijian endemic species and Solomon Islands-Papuan fauna, with a tendency for Papuan-derived groups to gradually diminish eastward. *Xanthagrion erythroneurum* Selys, 1876 and *Tramea eurybia* Selys, 1878 from Taveuni are given as examples of the strong Australian connection (Donnelly 1987).

Donnelly (1986) pointed out possible pathways by which the new colonists have invaded the Pacific islands and especially Samoa. Young islands are characterised with lentic habitats, while lotic waters are mainly ephemeral. Therefore, the suggestion is that sea-level ponds were occupied first, with secondary spread into upland stream habitats occurring later. In another view of the Samoan fauna, Fraser (1927) identified all Anisoptera as immigrants with the exception of *Hemicordulia* and *Gynacantha*. He assigned various sources of origin, mainly Australia and New Guinea.

All of the Cook Islands Odonata have been treated as recent immigrants that have spread to these islands through the air and have a wide distribution (Lieftinck 1953).

For the eastern parts of Polynesia there are little data. Englund & Polhemus (2010) suggested that endemic damselflies of the Austral Islands may be remnant representatives of the stocks that initially colonised what is now French Polynesia (but did not say from where), and potentially gave rise to the subsequent radiations that arose on islands to the north and east. According to Polhemus et al. (2000), Marquesan taxa are insular derivatives of an ancestor from the Philippines and New Guinea.

Despite the large literature on the topic, though, the truth is that no study on Pacific islands Odonata provides any empirical evidence on the reported power of dispersal. Studies have mainly focused on fauna and taxonomy with little biogeographic analyses. Where analyses were carried out, they were usually done at a preliminary stage with insufficient faunistic data and only vague statements about the origin of the Pacific fauna. The hypotheses proposed for Pacific Odonata biogeography were largely based on the inferences from the known distribution. However, assumptions based on distributional data alone are bound to be imprecise (Waters & Wallis 2000). This is especially true for groups where the uncertainties around the taxonomy are as high as they are in Pacific Odonata (Marinov & Pikacha 2013).

Pacific species from the area surveyed here (see Material and Methods) have rarely been used in morphological or molecular phylogenetic studies. In studies on the entire order, Bybee et al. (2008) included the highest number of Pacific species – just five: *Hemicordulia australiae* (Rambur, 1842), *Isosticta robustior* Ris, 1915, *Caledargiolestes uniseries* (Ris, 1915), *Caledopteryx maculata* Winstanley & Davies, 1982 and *Trineuragrion percostale* Ris, 1915. Three more were analysed in Rehn (2003): *Austrolestes colensonis* (White, 1846), *I. aurora* and *Pseudagrion microcephalum* (Rambur, 1842). Dumont et al. (2010) added *I. aurora* too to the phylogeny of the entire order too.

In a comparative phylogenetic analysis of Anisoptera, Fleck et al. (2008) included *Uropelata carovei* (White, 1846) and *Agrionoptera insignis* (Rambur, 1842). Dijkstra et al. (2014) incorporated ten Pacific taxa (*Caledopteryx sarasini* (Ris, 1915); *Caledopterys* sp.; *T. percostale*; *Isosticta gracilior* Lieftinck, 1975; *Isosticta* sp.; *Teinobasis rufithorax* (Selys, 1877); *Austroagrion watsoni* Lieftinck, 1982; *Xanthagrion erythroneurum* Selys, 1876; *Agriocnemis femina* (Brauer, 1868) and *I. aurora*) in their phylogenetic tree of the Zygoptera and commented on the taxonomic position of other Pacific genera as well.

Ware et al. (2007) analysed only two New Zealand species, *Procordulia smithii* (White, 1846) and *Procordulia grayi* (Selys, 1871), in the phylogeny of Libelluloidea, while the representatives of this superfamily account for about 40% of the Pacific Odonata fauna.

In the studies at family level, von Ellenrieder (2002) included *Anax papuensis* (Burmeister, 1839) in the phylogeny of Aeshnidae; O'Grady & May (2003) analysed *Agriocnemis femina*, *A. pygmaea*, *Nesobasis erythrops*, *Xiphiagrion cyanomelas*, *I. aurora* and *Amorphostigma armstrongi* of Coenagrionidae and Ware et al. (2014) studied *U. carovei* of Petaluridae.

It is evident that only 22 taxa (10%) of the Pacific Odonata have been incorporated in the phylogenetic studies. Of these only 14 taxa (6%) are endemic to the Pacific while the others are widespread species that enter the investigated area, but have not been sampled from within it.

Scanty information on species biology and ecology is another factor hindering the study of Pacific Odonata biogeography, because relationships between organisms and their natural environment can be used to generate broad biogeographic predictions (Gillespie et al. 2012). Studies on Pacific Odonata biology and ecology are well documented for New Zealand only (Rowe 1987). Van Gossum et al. (2007; 2008) and Beatty et al. (2007) studied the biology of selected species in the Fijian endemic genus *Nesobasis* Selys, 1891. Dumont & Verschuren (1991) and Moore (1993) investigated the atypical behaviour of *P. flavescens* from Easter Island. Information about other island groups is scattered in faunistic and taxonomic studies.

Plausible biogeographic predictions must rely on research that distinguishes between indigenous and introduced species (Gillespie 2007). Unfortunately, historic aspects have never been considered in the literature on Pacific Odonata, except for New Zealand. Earlier explorers have entered the Pacific island region at time when there was already intensive transport of goods between Pacific nations, and biosecurity was not of high concern. Schabetsberger et al. (2008) wrote on the influence of WWII and the large-scale transport of military equipment inevitably led to intensive exchange of organisms between islands. Unfortunately there is no way to investigate the faunistic composition of the islands prior to their exhaustive exploration at the beginning of the twentieth century.

If such powerful fliers as *P. flavescens* is believed to have been transported to the Easter Islands by humans, why do we accept that such delicate species as *I. aurora* have been self-dispersed across the Pacific with aerial dispersal as the only way to occupy the islands? *Xiphiagrion cyanomelas* Selys, 1876 is another very small, delicate species considered to be wind-borne (Lieftinck 1968); but why did it not disperse further east than the Solomon Islands? Moreover, how do we know that wind mediated, long-distance dispersal has actually happened? We do know that by the mid-twentieth century one species (or a complex of related species) was distributed across the entire ocean, but does this mean they were there at the beginning of the century? With a complete lack of morphological and molecular phylogenies for the Pacific species, how do we know which species have dispersed from where? What is the geological evidence for the existence and location of earlier islands in the Pacific?

These topics are reviewed here in the light of seven “oddities” seen in the Pacific Odonata. Those are facts from the current species distribution that cannot be explained by simple aerial dispersal alone. An alternative model is suggested which considers the composite influence of Pacific geology, Odonata biology and ecology, and anthropogenic factors.

Material and Methods

A complete collection of references to the Pacific Odonata has been databased and is free available on request. The taxonomic and faunistic assessments were prepared by Marinov et al. (in prep./b) as part of a project on spatial modelling of the Pacific Odonata habitats (Marinov & Doscher 2011).

In the present study the same literature sources were re-examined, with particular attention given to the biogeographic analyses presented by previous researchers. These were reviewed in the light of other evidence from biogeography and geology to propose new models on the palaeogeography of the Pacific Ocean. Opposing views have all been considered in examining certain aspects of the current Odonata distribution.

The study area discussed here (Fig. 1) is the same one used by Marinov & Doscher (2011) in their study modelling Pacific Odonata habitats. It includes the area bounded by Macquarie Island and the Mariana Islands in the west, and Easter Island in the east.

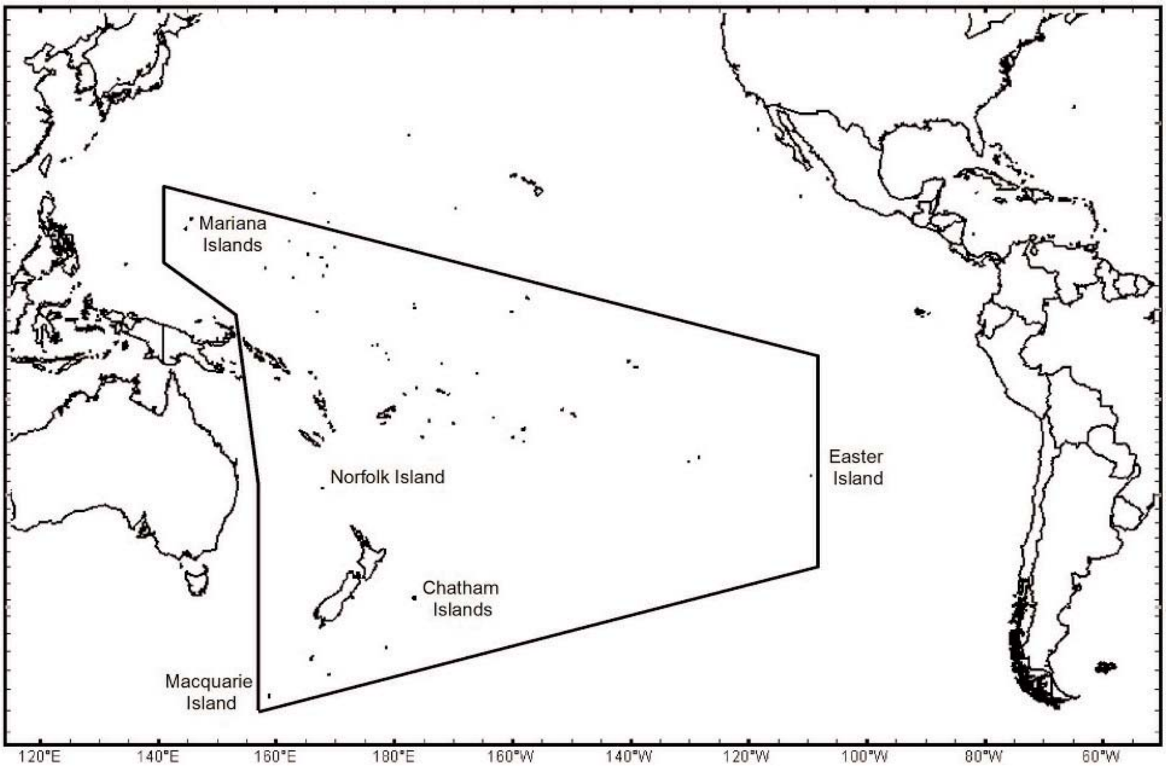

Figure 1. Study area established for the Pacific Odonata modelling scheme.

Explanations of terms

The literature on the biogeography of the Pacific Odonata indicates that there is no unified terminology to denote concepts such as dispersal and long-distance. Dispersal is rarely defined and usually people accept that species that move across land/sea areas are dispersive, regardless of the distance they move. In a recent review of long-distance dispersal, Gillespie et al. (2012) defines dispersal as “unidirectional movement of an individual from its place of birth”. However, in population genetics, dispersal is viewed not just as one way translocation, but as movement of individuals between demes (Ibrahim et al. 1996). In a study of movement strategies for short- and long-distance dispersal in *Coenagrion mercuriale* (Charpentier, 1840), Keller & Holderegger (2013) followed Clobert et al. (2009) in defining dispersal as “... the active or passive attempt to move from a natal or breeding site to another breeding site.” Hargreaves & Eckert (2013) added to this definition that a “… successful dispersal requires that individuals reproduce after they have moved.” In this sense, a flying individual away from the breeding ground (over land or sea) could not be considered as dispersing, unless there was good evidence that once it has moved it will successfully breed in a new site. Likewise, species migrations from breeding areas to wintering grounds and back again would also be excluded from the category of ‘dispersal’, in spite of the incredible distances covered.

Migrations in Odonata have been reported for a number of species. Most of the records, however, are on individuals flying over land. *Anax junius* (Dury, 1773) changes its migration route by more than 120° upon reaching an ocean barrier, evidently reorienting in response to landmarks (May 2013). While in the air the habitat connectivity on the ground possibly gives the migrating insects security in their determination for flying over long distances. Insects migrating over oceans, unlike migrating birds cannot rely on the experience of their parents. Therefore, taking on a journey over inhospitable and hostile environment that has nothing to do with their natural habitat is a mystery that still has no convincing explanation. The end of this flight is also unpredictable. Yamane & Hashiguchi (1994) report on *P. flavescens* approaching the sea water at the Sato-mura, Kami-Koshiki-jima Island, Japan and literally diving to death. Individuals did not fly away and even when picked up and released went to the sea again. Another report on the same species noted that the power of migration was completely lost once individuals settled on Easter Island, where they are the only Odonata present (Dumont & Verschuren 1991). Individuals from the local population are poor flyers, showing a tendency to aggregate and forage in windsheltered areas, and displaying a perching reflex in sudden gusts of wind. However, a later study (Moore 1993) established that *P. flavescens* from Easter Island did not differ in behaviour and morphology from its counterparts worldwide.

Other terms apart from 'dispersal' have been used interchangeably to describe changes in spatial positioning. Khelia et al (2014), for example, speak of displacement, long-range movement, long-distance movement and long-distant dispersal as synonyms in their study of the biology of *Calopteryx exul* Selys, 1853. It is, however, important to establish when the distance that an individual passes in this dispersal should be considered short and when it becomes long. In the same study Khelia et al. (2014) consider movement at 5.3 and 4.9km as a long-distance because normally *C. exul* moves about 50m between perching sites. For *C. mercuriale* Keller & Holderegger (2013) defined any flight along a stream as 'short-distance' movement (these were normally under 300-500m) while a flight in a straight line crossing agricultural land (usually under 4.5km) was regarded as 'long-distance'.

These two examples show how ambiguous the terms short- and long-distance can be depending on the individual species' typical biology pattern. We cannot apply the same definitions to the Pacific Odonata, because distances of about 5km are negligible in this vast region. However, we can perhaps consider as 'long-distance' any movement of a species across atypical habitat, such as agricultural land in the above example. For the Pacific Odonata it would involve crossing sea water. Therefore a flight to Aunu'u Island just 1km off from Tutuila Island, American Samoa should be considered as a long-distance event. However, for such powerful flier as *P. flavescens* or *Tramea transmarina* Brauer, 1867, both common inhabitants of Aunu'u Island, a distance of 1km is not far (Johansson et al. 2009).

At about 100 Ma the block of continental crust later separated as Zealandia (Mortimer 2004) was still part of Gondwana. It was not a problem for dragonflies at that time to pass over to what later became very distant land masses – Australia, New Guinea, SE Asia at the western end and New Zealand, New Caledonia and Norfolk Island at the eastern. After continental drift began though, there was a moment in the geological history when the drifting land masses were so far apart that insects could not easily travel to exchange genes and support phylogenetic coherence.

Finding this crucial distance would define the long-distance movement which could lead to dispersal in the biogeographic sense.

In a willing flight between two land masses visual clues would probably play a significant role. Baird et al. (2010) demonstrated that the bumblebees, as with honeybees and *Drosophila* flies, rely primarily on visual cues to regulate their ground speed. The pattern of visual motion generated during flight, also known as optic flow, is used by insects to orient their flight. Therefore, an island in the sea not visible to an observer on the ground may become partly visible to an air-borne insect when the angle of the visual field changes and gives wider perspective. Otherwise for the transportation between two land masses insects have to rely on passively mediated displacement by winds.

Wind as a dispersal mechanisms for insects

In 1957 scientists from the Bishop Museum, Honolulu, developed a method for trapping insects at high altitude over the ocean (Holzapfel et al. 1970). A summary of the collecting equipment and a summary of the insects reported from 1957 through 1966 is presented in Holzapfel & Harrell (1968). This is a detailed report on an expensive 10-year programme which made important inputs to the studies of air-borne insects found within the Pacific. Holzapfel & Harrell (1968) examined four possible ways insects could be carried among the islands: 1) wind, flight, or both; 2) marine drift; 3) birds, or bats, and 4) man.

Holzapfel & Harrell (1968) argued that once caught in the air and lifted upwards by thermal convective currents of warm, rising air, insects are exposed to low atmospheric pressure, temperatures and moisture. The decreased temperature and moisture may render the insects immobile thus transforming them into particles passively transported by the wind. Low pressure in the atmosphere would increase the freefall of an inert insect. Therefore, air uplift would have little importance as a dispersal medium unless it was supported by horizontal transport across the ocean. However, these horizontal currents usually die down during the night, in which case the insect will fall into the sea. Holzapfel & Harrell (1968) cite experiments with balloons designed to study how much an insect is aided by convective processes. In one of the longest flights reported in Gaines & Ewing (1938), the drift was 600 km and took 18 hours and 11 minutes, with the balloon drifting at an average 48 miles/h. Therefore, Holzapfel & Harrell (1968) consider ordinary convection too weak to have any significant effect on the insect dispersal. For an insect to be transported in this way from New Guinea to the Marquesas (5,000 km) would require travel for 150 hours, which is nearly a week. Guppy (1925) doubted the possibility of direct aerial transport of insect as far as 3,500km, the distance from North America to Hawaii. Dumont & Verschuren (1991) also considered distances of 3,800km well above the dispersal capabilities of *P. flavescens*, which is otherwise notorious as a migrant (May 2013; Buden 2010).

Holzapfel & Harrell (1968) considered cyclones and hurricanes were more important for dispersal than ordinary convection. They argued that insects will not necessarily die when caught in the middle of a storm unless they have been trapped in the coldest part of it. Often viable insects were found thrown on the ground by cyclones. Hudson (1922) reported on hundreds of insects, including *P. smithii* and *Xanthocnemis zealandica* (McLachlan, 1873) covering the glacier surface on Mount Ruapehu, New Zealand. The insects were so numerous that they were initially taken to be a fine dust covering the glacier. Holzapfel et al. (1970) also established a relation between thunderstorms and insects flying in large numbers so close to a ship that they could be easily collected from the decks.

Cyclones strike the Pacific islands regularly. Lieftinck (1953a) reported on hurricane damage occurring in some parts of the Cook Islands group roughly once every two years, but the intensity is actually higher. Thompson et al. (1992) detected 107 cyclones for a study period of 10 years, with 48 of them becoming hurricanes (wind speed between 63 and 117 km/h). There was a maximum of 16 tropical cyclones in the 1982/83 El Nino year, and most of them were located around Vanuatu-New Caledonia. The same research established that the tropical cyclone season normally extends from November to April, with a maximum around February when the probability of major hurricane (wind speed greater than 167 km/h) is highest. Thompson et al. (1992) reported on the directions of the cyclones. Nearly 70% of them moved eastwards or recurved to east after initially moving west.

With a hurricane intensity of this magnitude, the Pacific island Odonata must have been regularly transported between archipelagos. Moreover, the cyclone season and the rainy season coincide with one of the best sampling periods for Odonata in the tropics (Clausnitzer et al., on-line publication). This would have hindered the discovery of endemism. However, endemic species are not just confined to specific archipelagos, but also to particular islands within the archipelagos.

Viti Levu and Vanua Levu are the two largest islands in Fiji and are situated just 45 km apart (even closer during Pleistocene glaciations; Neal & Trewick 2008). This should be a distance that is very easy for dragonflies to cross, given their often-cited powers of dispersal, especially if supported by the wind. Despite this prediction from theory, the islands in fact exhibit a high rate of endemic species in the diverse endemic genus *Nesobasis*. Including described species and new, undescribed species there are 12 species endemic to Viti Levu (Marinov & Waqa-Sakiti 2013) and 13 to Vanua Levu (van Gossum et al. 2008).

Holzapfel & Harrell (1968) found that the other two means of transport (marine drift and birds/bats hosts) have very minor importance for certain insect groups only – larvae in logs or soil dwelling insects and ectoparasites. None of these are considered further in the present study because Odonata larvae with a few exceptions are aquatic.

The final conclusion of Holzapfel & Harrell (1968), which is probably the only such an intensive study with review of transoceanic insect movement, was "... that today man is the primary agent in transporting insects from one land area to another."

Anthropogenic influence on insect dispersal

Williams (1958) emphasised that insects on a ship at sea may not be migrating/dispersing, but routinely living aboard the ship. Food and cargo loaded aboard may harbour certain species and while in port a ship “... may provide a haven from undesirable weather conditions or as desirable source of food, light at night, etc.” With no border restrictions until the middle of the twentieth century, and ships constantly crossing the Pacific for trade, military supplies or holiday cruises, many foreign organisms must have been introduced to new areas. Bunkers and other abandoned facilities from WWII are now frequently used as breeding habitats for Odonata on Tutuila Island (Marinov et al. in prep./a). Jackson (1968) gives an extreme habitat for Odonata on Engebi, the smallest islet of the Eniwetok Atoll, Northern Marshall Islands. Here, *P. flavescens* breeds in the ruins of an instrument bunker built for the nuclear test program. Accidental transport by man or birds to the islet was considered unlikely. Immigration from other less damaged islets was proposed as a more probable hypothesis for the origin of the breeding population.

A large ship departing from a port is attractive to many insects, including dragonflies, as it provides a large food supply and shelter. This is especially true for species that depart from their breeding habitats when they mature and find food sources along the waterfronts of Pacific port towns. In the widespread *Agriocnemis exsudans* Selys, 1877; *I. aurora*, *Hemicordulia hilaris* Lieftinck, 1975; *Diplacodes bipunctata* (Brauer, 1865); *Lathrecista asiatica* (Fabricius, 1798) and *T. transmarina* feeding has been observed along the waterfront of Nuku’alofa, Tonga, in two consecutive studies (M. Marinov, per. obs.).

Night cruises probably add an additional attraction because of the many light sources. This perhaps favours species, such as *Anaciaeschna jaspidea* (Burmeister, 1839) that often fly till dusk together with *Anax guttatus* (Burmeister, 1839) and *T. tillarga* (M. Marinov, per. obs.). Once the ship is in the open sea dragonflies find themselves trapped on board a small “island”. Nevertheless, cruises within the Pacific have never been considered important in the Odonata biogeography.

Biogeography revisited

Biogeography has three components – bios, “life”, geos, “Earth” and graphos, “description”. Deliberately or not, biologists dealing with biogeography often ignore theories about geological events. Studies mainly treat long-distance dispersal as the only possible way for colonisation of oceanic islands, whether by wind, migrating birds or sea rafting (Smith 2009). The ‘impossible” becomes very likely when reviewed in light of geological hypotheses about the history of the Pacific Ocean. Biologists also often take a snapshot of the present day species distribution ignoring historical data (or assumptions on past events), as well as what is known of individual species biology and ecology. A short review of these components is given next.

Species biology and ecology

Belyshev & Haritonov (1983) reviewed the topic of ageing in taxa. In a general sense, the life of a taxon may be compared to the life of an individual – with birth, growth and death. While still "young" the new taxon is 'eurybiont', and has high potential power to disperse and explore new environments. As the evolution progresses, the taxon becomes less of an "explorer" and more a "specialiser". Its demands for factors specific to the local environment increase and it becomes 'stenobiont'. At this stage of its "life" the geographical area and niche of the taxon shrink, and this creates opportunities for younger taxa to develop. *Uropetala chiltoni* Tillyard, 1921, for example belongs to Petaluridae which is considered one of the most primitive Odonata families (Ware et al. 2014) and includes some of the largest living Odonata (Rowe 1987). *U. chiltoni* inhabits very specific habitats: spring-fed bogs or swampy areas developed in tussock-covered faces of the foothills, where there is a permanent and consistent flow of water (Wolfe 1953).

Uropetala chiltoni may be one of the largest living odonates on Earth, yet most females only move a few hundred meters from their reproduction sites (Rowe 1987). On the other hand, the delicate *A. exsudans* disperse away from water in search of places to mature as reported by Marinov (2013) who established immature individuals more than a kilometre from their larval habitat. This raises another important aspect in interpreting biogeographic patterns – species mobility and diurnal activity. Large species may have a high potential for flying over long distances, but do they really do so in their everyday life? Fraser (1925), in contrast to most authors, considered that dragonflies, although strong on the wing, are extremely local insects, and he explained this by the fact that they are largely tied to their breeding places. In addition, large species may be almost inactive during the day and only fly at dusk (the behaviour is crepuscular; Corbet & Brooks 2008). Adults of the widespread *A. jaspidea* exemplify this behaviour. Usually during the day they remain low in the vegetation or pass swiftly across open areas with non-stop, direct flights (Marinov et al. in prep./a). At dusk, individuals appear in groups around the edge of wetlands (M. Marinov, per. obs.). *A. jaspidea* individuals also have been attracted to light sources (E. Edwards, per. obs.), probably in search of food. With such a typical behavioural pattern *A. jaspidea* cannot have spread throughout its present wide range unless actively flying or being passively transported during the night. If the first were true, the individuals would have had no visual clues for orientation, and it is highly unlikely that an insect would embark on a journey across the ocean without the assistance of the optical flow cited above. Transportation with cyclones is only possible when these strike during late evening or night and catch dragonflies on the wing. These two scenarios are applicable to other crepuscular species, such as *T. tillarga*. It is also widely distributed across the Pacific, but unlike *A. jaspidea*, individuals have been seen defending territories during the day and even during light rain in New Caledonia (M. Marinov, per. obs.).

Activity in Odonata even on rainy days has been commented upon by various researchers on the New Caledonian fauna. Davies (2002) reported that in New Caledonia he observed the highest number of species of Argiolestidae, Isostictidae and Synthemistidae during a persistent rain. Michalski (2013) explains a more complicated situation where field days resulted in almost no species in sunny days and success in cloudy days with light drizzle. He also experienced the opposite – lower

Figure 2. Arrangement of the continents in ancient Pangea according to the Plate Tectonic model.

number of individuals on cloudy days in comparison to sunny days. However, as a general rule Pacific Odonata, like all dragonfly species, avoid flying in the rain unless they are well sheltered in rock niches or dense tree canopies. This is seen in *Melanesobasis macleani* Donnelly, 1984 and *Nesobasis flavifrons* Donnelly, 1990 both from Fiji (M. Marinov per. obs.). *Orthetrum serapia* Watson, 1984 is one of the first species to disappear on a cloudy day from the wetlands on Savai’i Islands, West Samoa. Male *Rhyothemis regia chalcoptilon* Brauer, 1867 still defend territories on Aunu’u Island, American Samoa in light drizzle, but disappear on foggy, cloudy days (Marinov et al. in prep./a).

Geography of the Pacific Ocean

Biologists and geographers are sharply divided on the history of the Pacific Ocean (Adamson 1939). The Plate Tectonic model (Fig. 2) arranges the present day continents in a near compact landmass enclosed by an enormous ancient ocean known as Panthalassa (Wegener 1912). The idea was developed following advances in

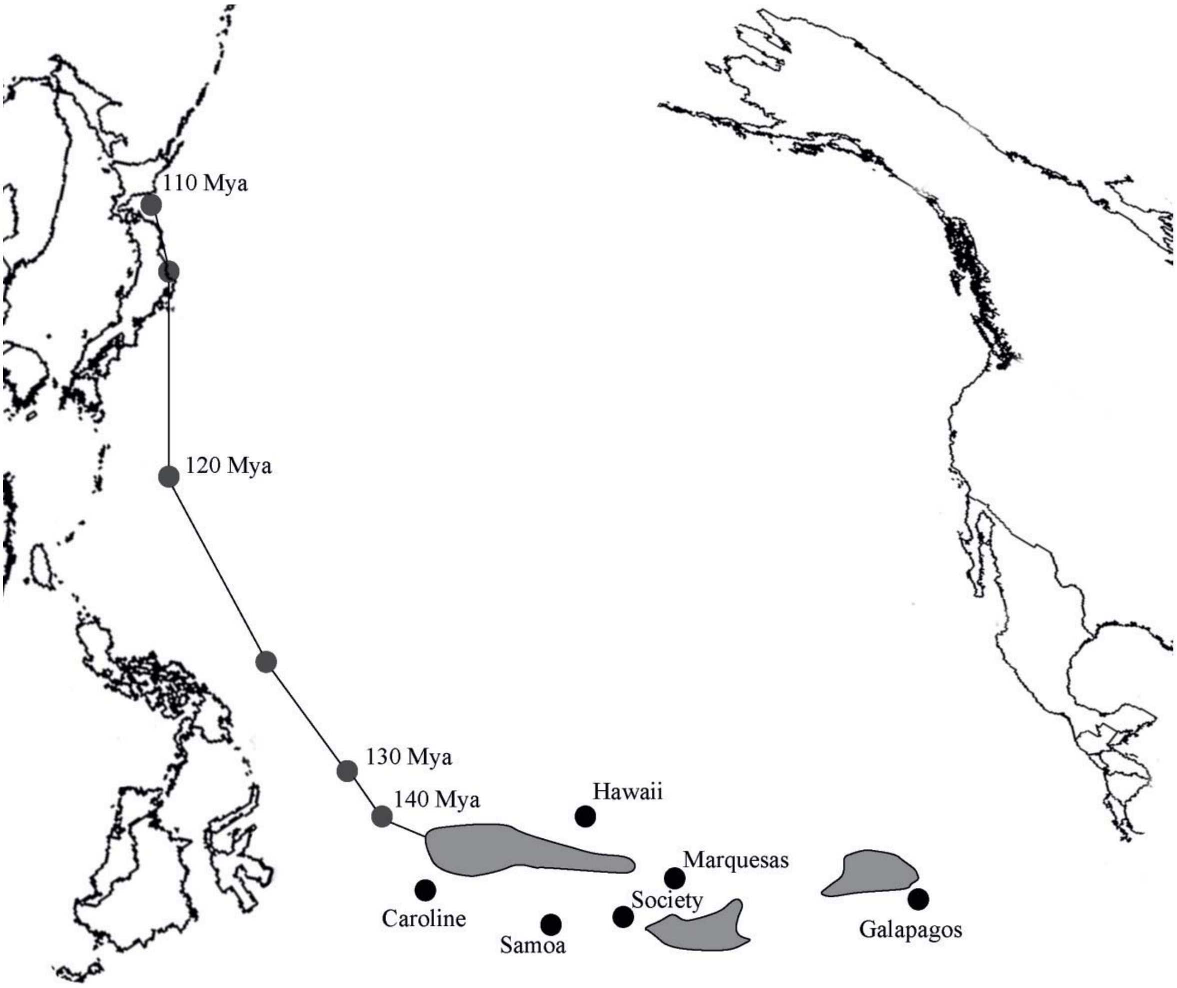

Figure 3. Paleogeographic reconstruction of the Panthalassa Super Ocean (modified from Kimura et al. 1994).

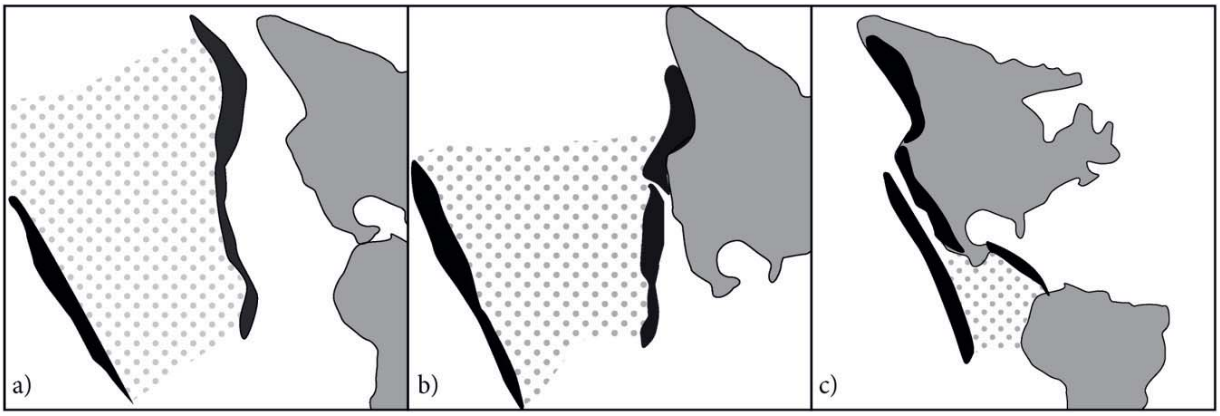

Figure 4. Island arc model for the Pacific origin of American terranes that progressively merged with North, South, and Central America between Mesozoic and Tertiary time (modified from Moores 1998): a) 180 Ma, b) 160 Ma, c) 100 Ma.

geology and geophysics, but was an old explanation for the great concordance between eastern South America and western Africa.

Neal & Trewick (2008) describe five major processes for formation of oceanic islands: volcanism and seamount building, atolls built up on the underlying subsided volcanic edifices, flexing of the lithospheric plate, rotation of fragments of the continental crust and island arcs on the Pacific margins. The final conclusion is that a part of Zealandia (see above) and all other islands in the Pacific have originated due to intraplate activities or motions along the plate boundaries.

In an earlier review of the Pacific islands, Shields (1976) revised information on the world's oldest islands (Oligocene or older) and cited studies that showed many of the Pacific archipelagos (e.g. Yap, Chuuk, Guadalcanal, Viti Levu, 'Eua, Lord Howe, Norfolk, New Caledonia, Espiritu Santo, Chatham, Moorea, Rapa, Marquesas (?), Easter (?), etc.) as having continental rock-types. By definition "continental rocks" include plutonic rocks such as granite and diorite and metamorphic rocks such as schist and slate. As a general rule such rocks are not found except on continents or on islands obviously once connected with continents. Therefore they all were considered as "...debris left from continental rifting prior to ocean basin formation by seafloor spreading."

Kimura et al. (1994) proposed a dynamic model for the formation of the so called "Sorachi Plateau" (now northern Japan and Sakhalin). In their study the origin of this plateau was traced back some 140 Ma in the middle of the ancient Panthalassa (Fig. 3).

In a similar manner Moores (1998) used geological evidence to propose the existence of two intraoceanic island arcs or archipelagos bordering an intraoceanic plate called "Cordilleria". The latter is suggested to have had an origin about 180 Ma west of the coast of North and South Americas (Fig. 4). Moving eastwards it collided with both present continents creating the long western mountain ranges.

Grehan (2001) used this view to explain the origin of the Galapagos fauna and the relations it has with Central-West Pacific and South American organisms. According to this theory an island arch (or arches) formed inside the Pacific away west of the American coast may have drifted eastward towards the content. During this movement, the arcs passed over a series of volcanic hotspots and their islands. The organisms moving with the arc were able to disembark on the islands once both were in contact (Fig. 5).

Shields (1979) suggested that the Pacific Ocean was closed at 155 Ma (Late Jurassic), an alternative to the plate tectonic theory arrangement of the continents in ancient Pangea (Fig. 6). McCarthy (2005) also provided biogeographical, palaeomagnetic and palaeosedimentary data supporting a closed Pacific with land connections in Late Cretaceous between Australia and East Asia, East Asia and North America, North America and South America, South America and Antarctica, and Antarctica and Australia. This view is termed the Expanding Earth (EE) theory (Fig. 7).

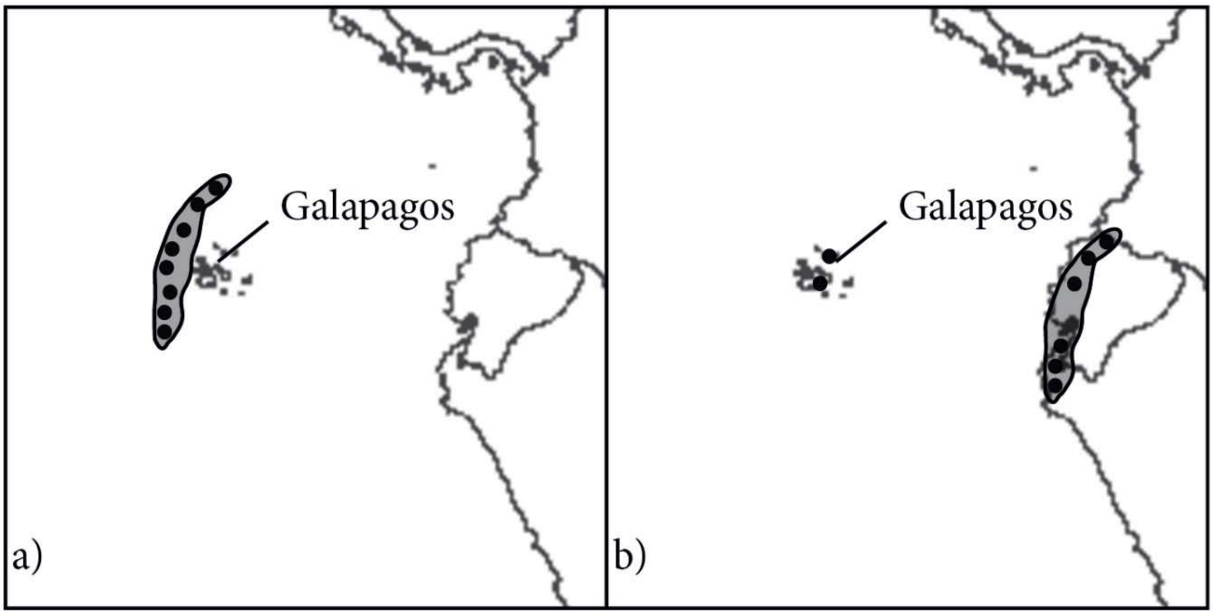

Figure 5. Paleogeographic model of the origin of the Galapagos biota: a) Cretaceous – an eastward moving island arc crosses the Galapagos hotspot allowing animals and plants (black dots) to colonise the volcanic landscapes, b) Present – island arc organisms are stranded at the Galapagos hotspot while their relatives are transported east and colonise the mainland (modified from Grehan 2001).

This is a small selection of studies that have proposed alternative models for the history of the Pacific Ocean. The present study does not follow any particular view, and it is worth bearing alternative scenarios in mind. It is also clear that geologists have not reached agreement on the locations of islands in the geological past. Many of the seamounts now under the sea level surely have formed as islands or archipelagos. As the sea level has risen above them they have "dispatched" their organisms to the neighbouring islands.

New islands are constantly appearing above the sea level even now. In December 2014 a new island was formed within the Ha'apai group of Tonga after the eruption of the Hunga Tonga-Hunga Ha'apai volcano. Figure 8 represents the situation before and after the eruption. Naturally, when the volcano cools down it will be populated by organisms from the two islands to which it is presently joined. If in the geological future those two islands for some reason subside there will be one island of young age, but old biota inherited from the neighboring islands existed in the past. It does not require dispersal from a source population situated on a continental landmass thousands of kilometres away.

When a new island appears in the middle of the ocean, dispersal is the only way for new organisms to establish on it, and they will come from a source population. However, the source may be a nearby island, and over time, taxa may "float" on younger stratigraphy (Heads 1990). Figure 9 illustrates the possible pathway for colonisation of oceanic islands following this model.

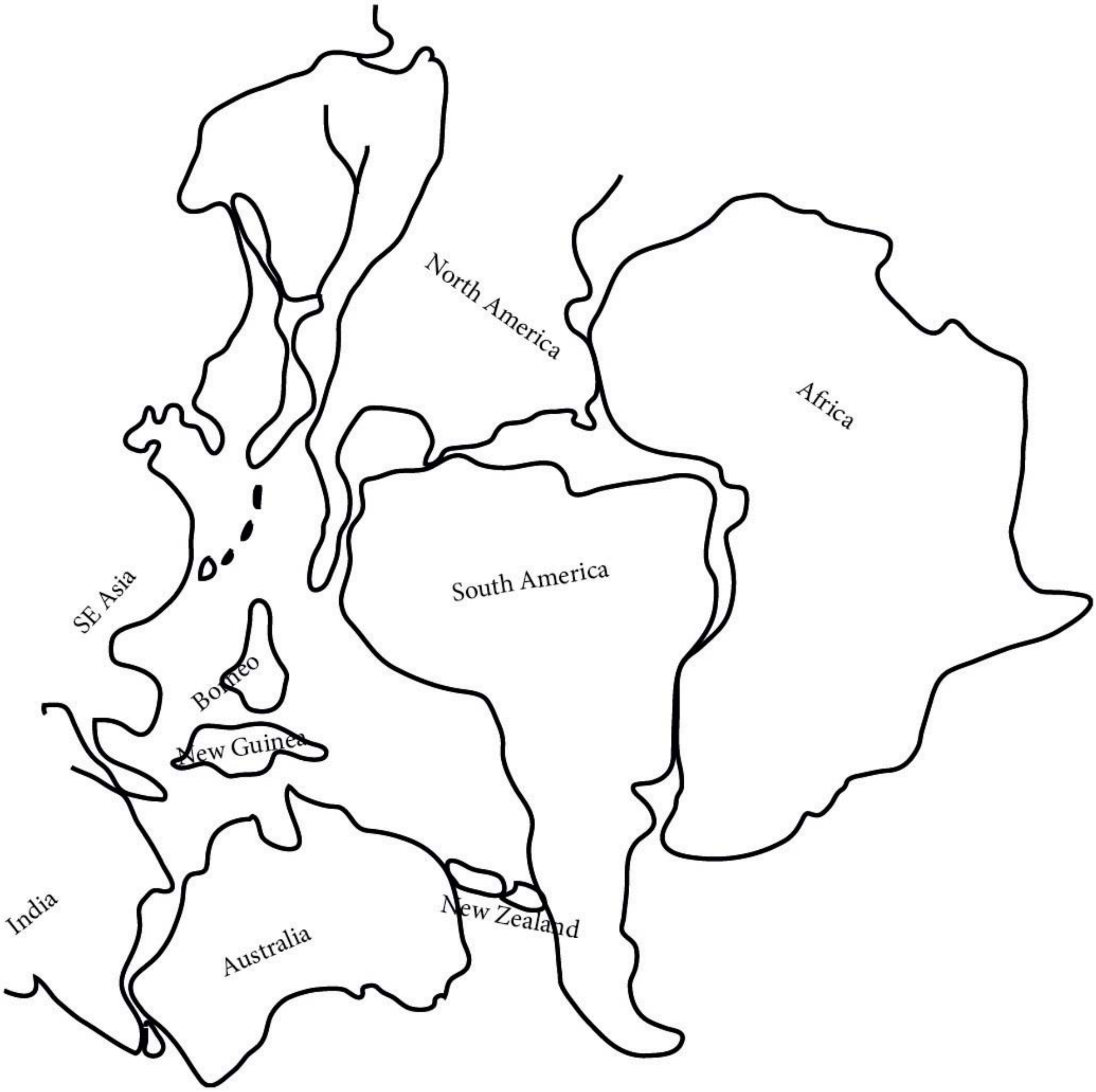

Figure 6. Peleogeographic reconstruction of a closed Pacific Ocean in Early Jurassic times (modified from Shields 1979).

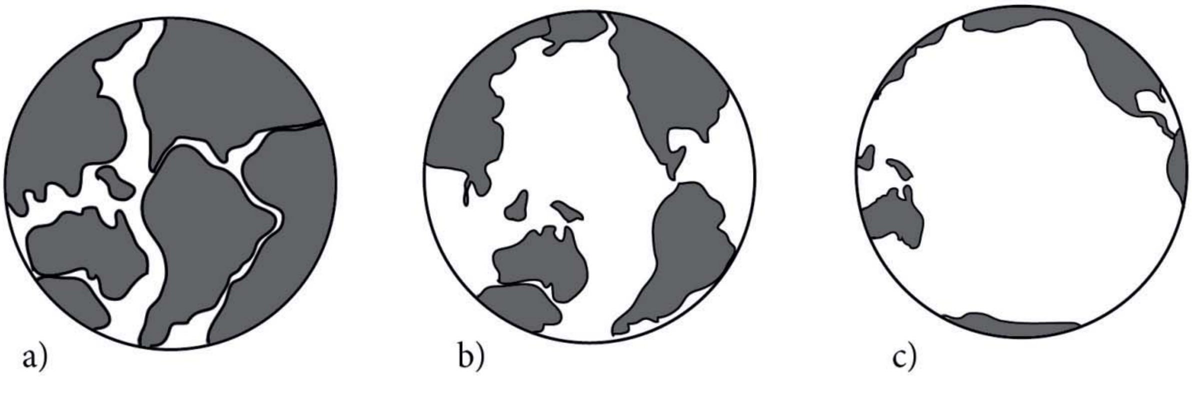

Figure 7. Expanding Earth evolution of the Pacific: a) Late Triassic, b) Late Cretaceous, c) present (modified from McCarthy 2005).

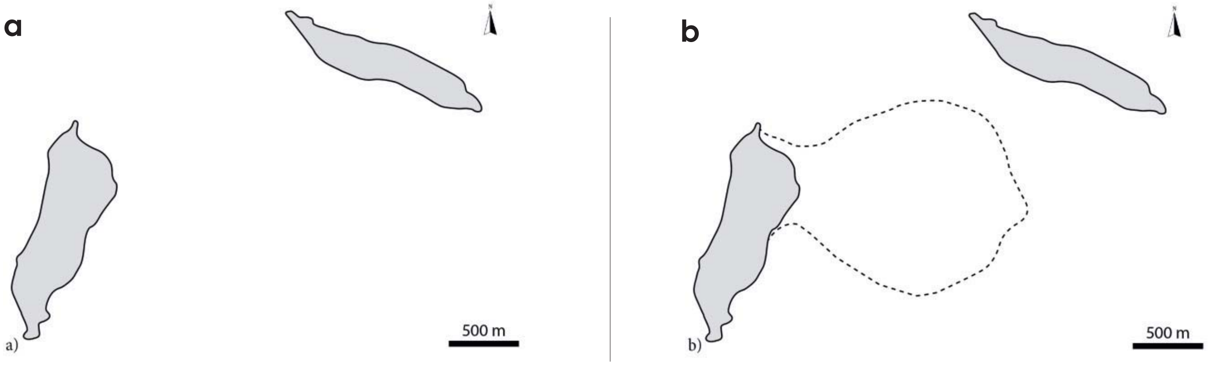

Figure 8. Formation of a new island in the Pacific after eruption of the Hunga Tonga-Hunga Ha'apai volcano: a) existing islands before the eruption; b) Island outlines after the eruption. Legend: dashed line indicates the position of the new island.

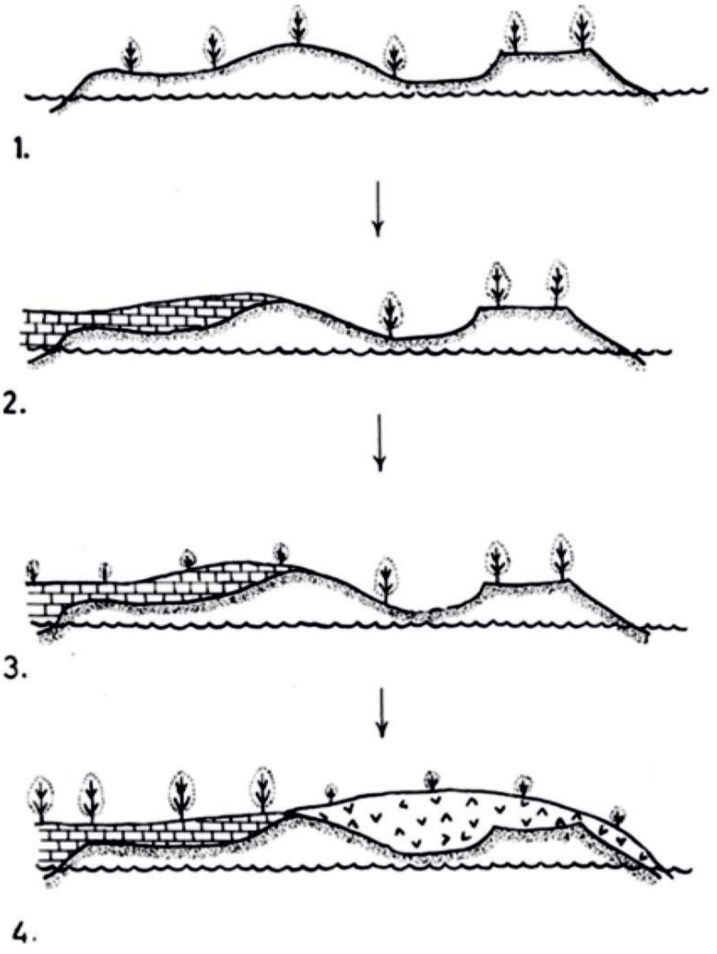

Figure 9. A hypothetical example to illustrate the process of old life "floating" on young stratigraphy. 1, A Mesozoic peneplain with ancient biota, represented by trees. 2, Mid-Tertiary marine transgressions and subsequent uplift has left much of the substratum covered with thick limestones. These are soon colonised by seedlings, shown in 3 and 4.

Combining undetermined data with the geological age of the islands only, creates an even larger ambiguity around the possible dates when the colonisation of the Pacific islands has happened and the pathways that have shaped the recent fauna. All islands move, by seafloor spreading. The oldest island in a chain gradually subsides as it drifts away from the place of its origin and becomes an underwater

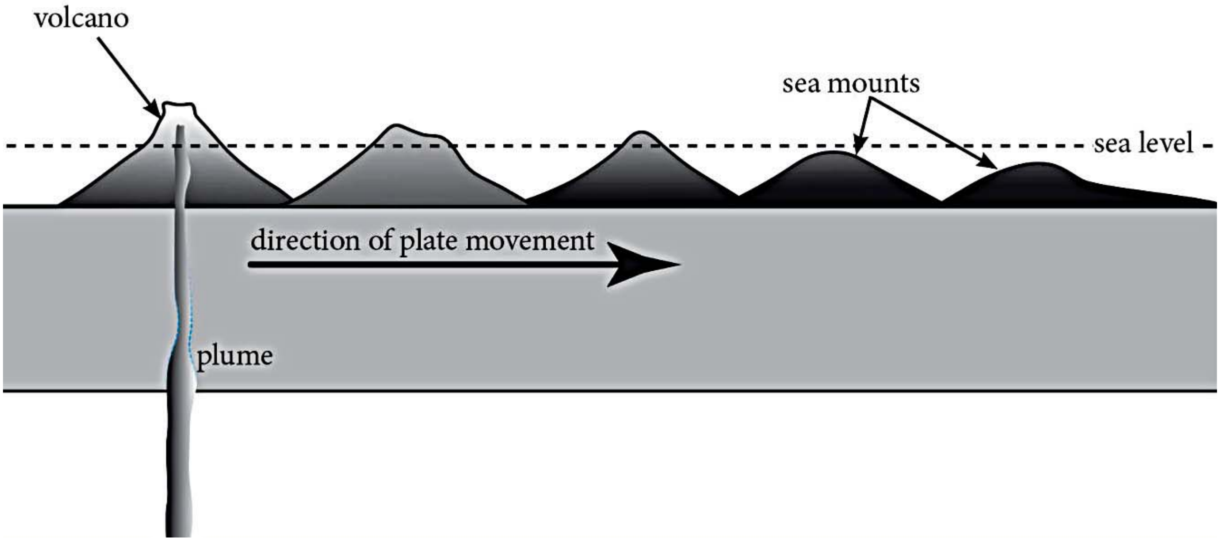

Figure 10. A model representing the role of the volcanic hotspots in formation and development of the islands.

seamount. At the moment it is on a position where a few million years ago there was another island from the same chain which is now long time gone under the ocean (Fig. 10).

Speculations in the Pacific Odonata biogeography

Examining the hypotheses of the origin of the Pacific Odonata it is evident that there is no clear evidence for transoceanic dispersal. The dispersal hypotheses were built on the distribution pattern without considering either the historical events (natural or anthropogenic) that may have influenced the species distribution, or relevant aspects of species biology and ecology. The main assumption has been that dragonflies are powerful fliers that are able to overcome long distances and settle in a new environment. This idea is fixed in the mind of anyone who has observed the extremely fast flight of dragonflies. It is so remarkable that people easily (and to some extend naively) divide Odonata into “...highly dispersive Anisoptera and the weakly dispersive Zygoptera” (Heiser & Schmitt 2013). However, even the dispersalists admit that: “… direct observations of the LDD are difficult, if not impossible for many taxa.” and “Actual observations of LDD remain limited … “ (Gillespie et al. 2012).

Obstacles for dispersing species

For successful establishment, dispersing species must overcome many obstacles – they need to survive for during the dispersal event (perhaps while exposed to extreme weather conditions), find mates to sustain a viable population, change their life style in a new environment, modify certain morphological features to adapt to the new habitat, and learn how to avoid new predators or parasites. For the success of a wind mediated dispersal, it is not sufficient just to have a strong wind to transport individuals. Charlesworth (2009) emphasized the importance of the number of dispersing individuals and the sex ratio, as these are crucial for viability of the future population. In the absence of constant immigrants, the pioneer individuals will form the initial gene pool, and hence assure, or not, long-term survival and evolution on the new island. There can be no doubt that genetic variation is related to population size (Frankham 1996). Lanfear et al. (2014) demonstrated that the rate of evolution is related to the effective population size (*Ne*), initially defined by Wright (1931) as the number of breeding individuals in an idealised population that would exhibit the same rate of heterozygosity loss over time as an actual population. Populations with small *Ne* and decreased genetic diversity will be less likely to adapt to future environmental changes (Bouzat 2010) as they have reduced evolutionary potential (Fisher 1958). Decreased *Ne* is associated with increased genetic drift (Beebee & Rowe 2008), which often results in increased homozygosity and loss of biodiversity (Lanfear et al. 2014) as the populations go through a bottleneck (Bouzat 2010). Migrating or dispersing organisms are likely to decrease individual's of its offspring's fitness (Lenormand 2002) moreover blown-by-the-wind individuals will find themselves in a completely new environment which will be an additional stress following that of the dispersal itself. Markert et al. (2010) established a considerably decreased population performance in a stressful environment for all levels of genetic diversity relative to performance in the permissive environment with 73% of the investigated populations going extinct.

Many of the insects caught in the middle of a storm will die and only a few survive. Whether this remnant will be enough to establish a viable population that will survive for millions of years and diversify, in the way we see in the Pacific Odonata, is another question. Transport of an individual insect by aerial currents will not yield any new population. Naturally, mating pairs must be formed by representatives of both sexes. However, the future development and genetic differentiation of populations depends on how colonising groups of individuals are formed and on the quantitative relationships between colonisation and migration (Wade & McCauley 1988). A single pair of insects or population with a small overall size (*N*) would not sustain a long term development without immigration from the source because of the inbreeding effect of their offspring (Beebee & Rowe 2008). Vucetich & Waite (2001) clarified that in real populations where $Ne/N < 1$ the required number of migrants to avoid excessive inbreeding is strongly dependent on size of the recipient population. This number increases dramatically as $Ne/N \ll 1$, which is a very likely scenario in a new colonization event where only a small proportion of the survivals the oceanic storm will probably be fit enough to breed.

Therefore, to be successful, transoceanic transport must happen periodically in the same direction for a number of years. Insects have a short life span, and if they do not die of exhaustion during the transport and somehow succeed in breeding and leaving offspring, the next generation will be mixture of inbreeding individuals. They will need new genetic stock in a short time if they are to survive. Slatkin (1981) demonstrated that the gene flow in natural populations depends on the geometric arrangement of demes and on the migration rates assumed for each deme. For Pacific Odonata living on isolated islands with no habitat connectivity in between for hundreds of kilometres, the geometric arrangement of populations is unfavourable for a constant gene flow relying on own power of dispersal unless supported by the wind currents. In the latter case we would observe nearly panmictic populations (Slatkin 1981) with a very low rate of endemism.

Another way of sustaining a long-term existence in an island group is by the transportation of a high number of individuals across the ocean from the source population. For the Pacific islands this number must have been so high that we now observe endemism up to genus level with 28.16% of the genera confined to particular island groups (Marinov et al. in prep.). Such a high number for the initial *Ne* (if only wind mediated) could have been achieved only by major storms.

However, dragonflies in the Pacific islands (and everywhere else in the world) would normally sense a coming storm and, unless caught in the air over the sea, will find shelter long before the storm hits. In this scenario the storm would need to be extremely powerful in order to rip the immobile dragonflies off the ground and transport them across the ocean to a new land. Even if it happened, it is unlikely that enough individuals for a viable initial population would be caught and survive the severity of the storm after hours of intensive swirling exposed to low pressure and freezing temperatures inside the cyclone.

Adapting to the new environment is the next obstacle for the colonists. Reduced dispersal abilities are often cited as a common feature of taxa on oceanic islands (Williamson 1981). For insects, wing reduction or complete loss of flight in some groups is cited as a typical response to strong winds or lack of natural predators (Gillespie 2007). Emberson (1995) reports that 90% of the beetle fauna of the Chatham Island is flightless. For dragonflies, flight is the main mode of locomotion, as species use their legs chiefly for catching prey, holding a partner during mating and clinging to the substrate when resting or perching (Suhling et al. 2015). Therefore, loss of flight would be fatal for them. Indeed, Marinov & McHugh (2010) established that Chatham Island endemic *Xanthocnemis tuanuii* Rowe, 1981 actually enlarged its wing area and thoracic capsule disproportionately to the overall body enlargement, which was attributed to the winds constantly blowing with up to 40km/h on the island.

Morphological changes like this do not happen in a few generations. Since the 2.5 Ma isolation of the Chatham Island from the main South Island of New Zealand, *X. tuanuii* has barely diverged from its congeneric *X. zealandica*. Precise morphometric and molecular studies were required in order to confirm the taxonomic status of the two (Amaya-Perilla et al. 2014). This raises important questions that apply to all occupants of new islands: (a) if reduction of flight abilities is really a response to the strong winds and the danger of the new comers to be blown back in the ocean, then did this danger persist from day one of the arrival or did it appear later? (b) if insects were exposed to constantly blowing winds, why were they not blown away on the next day or week while still so weak of exhaustion and not adapted to their new habitat?; (c) how did the new occupants survive for millions of years before they have adapted to the new environment without being blown out into the open ocean? (d) what was the driving force allowing a complete shift of the ecological and biological patterns for a short evolutionary period of time without recruitments from the source population?

Theory of the Island Biogeography applied to Odonata

Most biogeographers working on Odonata have been influenced by the widely accepted Theory of the Island Biogeography (MacArthur & Wilson 1967), which acknowledges that colonization from a mainland source population is the only means for occupation of volcanic islands by new organisms. Rates of colonization and extinction determine the taxonomic richness.

The theory of island biogeography does not refer to the important process, vicariance, or to human impacts in the formation of the island biota. The postulates of the theory raise two issues when applied to the Pacific Odonata: 1) if islands rely on species dispersal from a mainland, the new immigrants will be a subset of, or phylogenetically nested in mainland groups, and high-level endemism on the island will be low, and 2) extinct species must be replaced with others from the source population which infers a multiple colonisation events scenario.

Contrary to the first assumption, Marinov et al. (in prep./b) provide evidence for a very high rate of endemism in Pacific Odonata at various taxonomic levels. Endemic genera are known from Pohnpei Island (*Pacificothemis* Asahina, 1940), Solomon Islands (*Guadalca* Kimmins, 1957; *Lieftinckia* Kimmins, 1957; *Salomoncnemis* Lieftinck, 1987; *Solomonargiolestes* Kalkman & Theischinger, 2013; *Tapeinothemis* Lieftinck, 1950; *Wahnesia* Förster, 1900), New Caledonia (*Eoargiolestes*; *Caledargiolestes* Kennedy, 1925; *Caledopteryx* Kennedy, 1925; *Trineuragrion* Ris, 1915), New Zealand (*Antipodochlora* Fraser, 1939; *Uropetala* Selys, 1858; *Xanthocnemis* Tillyard, 1913), Vanuatu (*Vanuatubasis* Ober & Staniczek, 2009), Fiji (*Nesobasis*, *Hypothemis* Karsch, 1889), Samoa (*Amorphostigma* Fraser, 1925; *Pacificagrion* Fraser, 1926) and Marquesas (*Hivaagrion* Hämäläinen & Marinov, 2014). Endemism at lower taxonomic levels is even higher, with every Pacific archipelago having endemic species and subspecies. *Pseudagrion microcephalum stainbergerorum* Marinov, 2012 is endemic to Tongatapu where it inhabits the only marshland occuring on the island.

The transport of species from mainland source across the Pacific Ocean would tend to harmonise the fauna, especially if happens not as a single chance dispersal, but as a multiple event. As discussed above, it is highly improbable for an air current to support a viable founder population on a direct flight from a source population for 5,000 km, in order to reach such distant islands as the Marquesas in French Polynesia. Another possibility is that the Pacific islands received their Odonata species in a stepping-stone model of dispersal from the mainland. This predicts that phylogenies would show oceanic island groups nested within each other in a west-east direction (Kadmon 1995), and comparative phylogenetic analysis is highly desirable for the Pacific Odonata.

Van Gossum et al. (2008) tested the prediction that if dispersal played an important role in determining establishment success, the species found on smaller islands would comprise a subset of the more abundant species on the large islands. The results showed that *Nesobasis* of Fijian islands does not fully comply with this. *N. recava* Donnelly, 1990 of the small island Kadavu is not established on the nearest large island, Viti Levu (Fig. 11). The small Koro Island shares *Nesobasis* species mainly with the larger Vanua Levu, but also has *N. rufostigma* Donnelly, 1990, a species common on Viti Levu. The two largest islands Viti Levu and Vanua Levu have no *Nesobasis* species in common.

The long-distance dispersal scenario is supported by many contemporary molecular analyses that estimate clades to be younger than the oceanic islands they inhabit. The volcanic origin of some of the Pacific islands seems to favour the model of organisms dispersing from a source population on a mainland. A volcanic island with recent geological origin must have received its biota due to dispersal. However, terrestrial groups require land – not continental crust – and Heads (2012) reviews the evidence that there was always land within the Pacific in form of islands. He commented on the autochthonous nature of the Pacific groups and implicitly accepted the metapopulation model suggested by Hjerman (2009) as more applicable to the origin of the Pacific taxa. The metapopulation concept was developed in

Figure 11. Distribution of the Fijian endemic *Nesobasis* and species shared between the main islands within the archipelago. *Nesobasis* f. and *Nesobasis* v. refer to discovered species that has not been described yet.

studies on disjunct populations of terrestrial animals and plants which exist in separate patches of suitable habitat. In this way they populate "islands" on the mainland that are spatially isolated by areas of unsuitable habitats, in a similar way in which oceanic islands are separated by sea water.

A complete map of the seamounts of the oceanic floor is not available yet. Allain et al. (2008) summarised information from 20 seamount databases and produced a final list of 4021 underwater features. Even with this imperfect information, it is clear that the Pacific Ocean has large areas of seamounts that extend from the emergent islands in various directions. Many of them have been emergent islands in the geological past, with their own evolutionary history.

The application of molecular techniques

The growing acceptance of long-distance dispersal as the only mode of colonisation of new islands is backed up by data from molecular clock studies, a technique that has been welcomed by many biogeographers searching for estimates of clade divergence times (Kumar 2005). If molecular clock ages for clades are younger than the opening of seas or emergence of islands, dispersal is accepted as the only logical explanation for the contemporary species distribution. For example, Trewick (2000) established that there were low genetic distances between flightless insects inhabiting Chatham Island and their counterparts on the New Zealand main islands. He argued that phylogenetic separation between the two island populations could only be the result of long distance dispersal because the low genetic distance indicated a young age, younger than any possible vicariant processes. However, genetic distances are rather crude indicators of evolutionary history (Pybus 2006). A short genetic distance between two sequences may suggest a recent common ancestor, but it is also consistent with a slower rate of sequence change and a more ancient common ancestor. Pybus (2006) continues that "Evolutionary rates depend on a combination of factors: generation time, population size, metabolic rate, the efficacy of DNA repair, and the degree to which mutations are beneficial or deleterious, all of which may vary among species". Therefore, a prior calibration of molecular clocks is a crucial step before they are deployed (Warnock et al. 2012). In a number of studies, summarised in Heads (2012, 2014), three main methods for calibrating molecular clocks have been adopted, but all have problems:

- use the oldest fossil of a group; but this only gives a minimum age for the group;
- use the age of the island or the strata that a group is endemic to; but young islands and strata often have old taxa, and
- correlate the geographic distribution of a group with associated tectonic events; but tectonic features can be reactivated at different times.

The importance of the geography in species distribution and evolution

Overlooking relevant events from Earth history is a potential pitfall for every biogeographer. In their theory of island biogeography, MacArthur & Wilson (1967) did not consider vicariance. In fact vicariance was not mentioned as playing any role in shaping the contemporary species distribution at all.

However, in the early twentieth century, long before the invention of the Theory of Island Biogeography, specialists on Odonata began to discuss possible land connections between west Pacific islands and Australia, and the idea of a former, ancient continent that is now submerged. With the exception of *Hemicordulia* and *Gynacantha*, Fraser (1927) considered all Samoan Anisoptera to be immigrants. But for *Hemicordulia* he suggested a possible origin on an ancient, now-submerged Western Pacific continent. Tillyard (1912) accepted the presence of *H. australiae* on the Kermadec Islands as evidence for a land connection with Australia in post-Miocene time. Tillyard (1924) accepted that Fiji was part of an old continental mass bordering the Pacific Ocean.

These views have been largely forgotten as implausible. Lieftinck (1953) disagreed with Tillyard's (1912) theory on the grounds of the observed mass occurrence of *H. australiae* in the lowlands of New Zealand. During his visit in 1949 he found *H. australiae* to be one of the most common dragonflies, and he concluded that the observed abundance was good evidence for self-introduction. However, studies have shown that vicariance on fragmented island arcs, such as the Vitiaz Arc (Solomon Islands, Vanuatu, Fiji) have been important in the Pacific (Heads 2012). This view has to be remembered when considering biogeography in Pacific Odonata.

Moreover Lieftinck visited New Zealand in a time when, as obvious from historical data, the species had been already well established in the country. An earlier visit, for example, beginning of the century, would have yielded no detections at all. This is a good example of the importance of keeping track of the historic data.

The importance of historic records

Most studies on Pacific Odonata have relied on contemporary distribution patterns, and the authors have adopted the notion of wind-borne, long-distance dispersal without considering the possible significance of historical events. Unlike other Pacific region New Zealand has a very long history of odonatology. Thanks to the intensive field collection of Dr John Armstrong we have a well-preserved documentary of the colonisations of three species (*I. aurora*, *Anax papuensis* (Burmeister, 1839) and *H. australiae*) that took place in the 1920s-1930s (Armstrong 1958a, b; 1978). Rowe et al. (2011) reported on *Tramea loewii* Kaup in Brauer, 1866 as another recent arrival to New Zealand. All four Odonata species are considered as self-introduced for the last 80-90 years although Tillyard (1912) considers both *H. australiae* and *A. papuensis* as non-migratory. An obvious question arises here: why did these species disperse now? Why, when they have been around for hundreds of thousands of years, did the species wait for so long and invade New Zealand only in the last 80-90 years? Note that one of the species, *I. aurora*, is one the most widely distributed species throughout the Pacific, and because of its small size it is almost always considered as an obligatory air-borne species. Considering the history of invasion documented by Armstrong, New Zealand Odonata biogeography would have looked very different at the beginning of the twentieth century. Table 1 shows that prior to XXth century the endemism was as high as 80% (including the later described *U. chiltoni* and *X. tuanuii*). Tillyard (1926) reported on both *I. aurora* and *H. australiae* as "occasionally taken in New Zealand", which gives an indication of the approximate time of the invasion. If we consider *Diplacodes bipunctata novaezealandiae* McLachlan, 1894 as an endemic subspecies the percentage of endemic taxa would be even higher. *Aeshna brevistyla* Rambur, 1842 on the other hand has never been compared to its counterparts from Australia and New Caledonia. Davies (2002) described *A. b. caledonica* subsp. nov. for the New Caledonian populations. According to Tillyard (1912), New Zealand representatives of *A. brevistyla* differ from Australian ones being smaller and darker. He did not find differences between New Zealand and Kermadec populations, and this has been confirmed later in Armstrong (1973). Further morphological analysis on *A. brevistyla* is indeed needed, but this indicates that the New Zealand Odonata fauna of the early twentieth century may have been 100% endemic.

Table 1. Chronology of New Zealand Odonata records.

Species	Endemic	Reference
Austrolestes colensonis (White, 1846)	yes	White (1846)
Procordulia smithii (White, 1846)	yes	White (1846)
Uropetala carovei (White, 1846)	yes	White (1846)
Antipodochlora braueri (Selys, 1871)	yes	Selys (1871)
Procordulia grayi (Selys, 1871)	yes	Selys (1871)
Aeshna brevistyla Rambur, 1842	no	McLachlan (1873)
Xanthocnemis zealandica (McLachlan, 1873)	yes	McLachlan (1873)
Diplacodes bipunctata (Brauer, 1865)	no	McLachlan (1894)
Uropetala chiltoni Tillyard, 1921	yes	Tillyard (1921)
Hemicordulia australiae (Rambur, 1842)	no	Tillyard (1926)
Ischnura aurora Brauer, 1865	no	Tillyard (1926)
Pantala flavescens (Fabricius, 1798)	no	Anon. (1950)
Anax papuensis (Burmeister, 1839)	no	Armstrong (1958a)
Xanthocnemis tuanuii Rowe, 1981	yes	Rowe (1981)
Tramea loewii Kaup in Brauer, 1866	no	Rowe et al. (2011)

Are the naturalized Odonata the result of self-introduction or of man-assisted transport? The increased trade between New Zealand and the rest of the world in the early twentieth century suggests the latter. The New Zealand Ministry for Primary Industries has a large database with interception records of any organisms at the border dating back to fifties-sixties, and Odonata have been discovered in imported containers. Unfortunately we can only speculate about the origin of the insect fauna before that date.

In another interesting example, Endersby (2002) considered the arrival of such widespread species as *P. flavescens*, and possibly *Anax* and *Diplacodes* (sight record only; not collected) on Norfolk Island to be more recent. These are all conspicuous and should have been noted by earlier explorers of the island. However, none of the previous coleopterists or lepidopterists reported any of these dragonflies, and none were recorded in two studies specifically dealing with the Odonata of Norfolk Island (Smithers 1976, 1998).

Concluding remarks

Most of the speculations about Pacific Odonata biogeography seem unfounded without the back up of morphological or molecular phylogeny, and before the completion of the taxonomical studies. No comparative analyses have ever been performed with a focus on Pacific taxa. Earlier biogeographic analyses were restricted mainly to particular archipelagos. They were highly influenced by the Theory of Island Biogeography and did not consider important aspects of the geography of the Pacific Ocean, as well as individual species biology and ecology, historical data and human influence.

Seven “oddities” in the biogeography of Pacific Odonata

Analysis of the existing taxonomic and faunistic information on Pacific Odonata indicates seven phenomena that cannot be explained by random gene transfer mediated by wind dispersal over large distances. The seven phenomena appear to be “anomalies” associated with the Pacific Islands dragonflies. “Anomalies” is used to denote differences between the distribution patterns and faunal composition of Pacific species compared to those of their counterparts from the rest of the world. (The ‘anomalies’ are simply regular consequences of the past geological and evolutionary events that we do not understand well enough). Those are odds that should not exist having in mind the great potential for long-distance flight ascribed to the dragonflies.

1. Very high rate of endemism. Endemic species develop in isolation and with breaks in gene flow for long periods of time. Being powerful fliers that cross ocean barriers, dragonflies should have low levels of endemism. In fact, high levels of endemism are observed in Pacific Odonata and these are inconsistent with the inferred power of aerial dispersal. Heavy storms, if responsible for the initial transportation of individuals from the source population, would also bring more individuals periodically, and this would gradually harmonise the populations. This is not seen in Pacific odonates, however, as the group shows high levels of geographic structure.
   For example, the genus *Pacificothemis* Asahina, 1940 is endemic to the small island of Pohnpei (Asahina 1940). Asahina (1940) also described endemic *Hemicordulia* species in the Caroline Islands, Micronesia and commented on their distribution. Geologically older islands have their own endemic species, with *H.*

Figure 12. Distribution of endemic *Hemicordulia* species within the Caroline Islands.

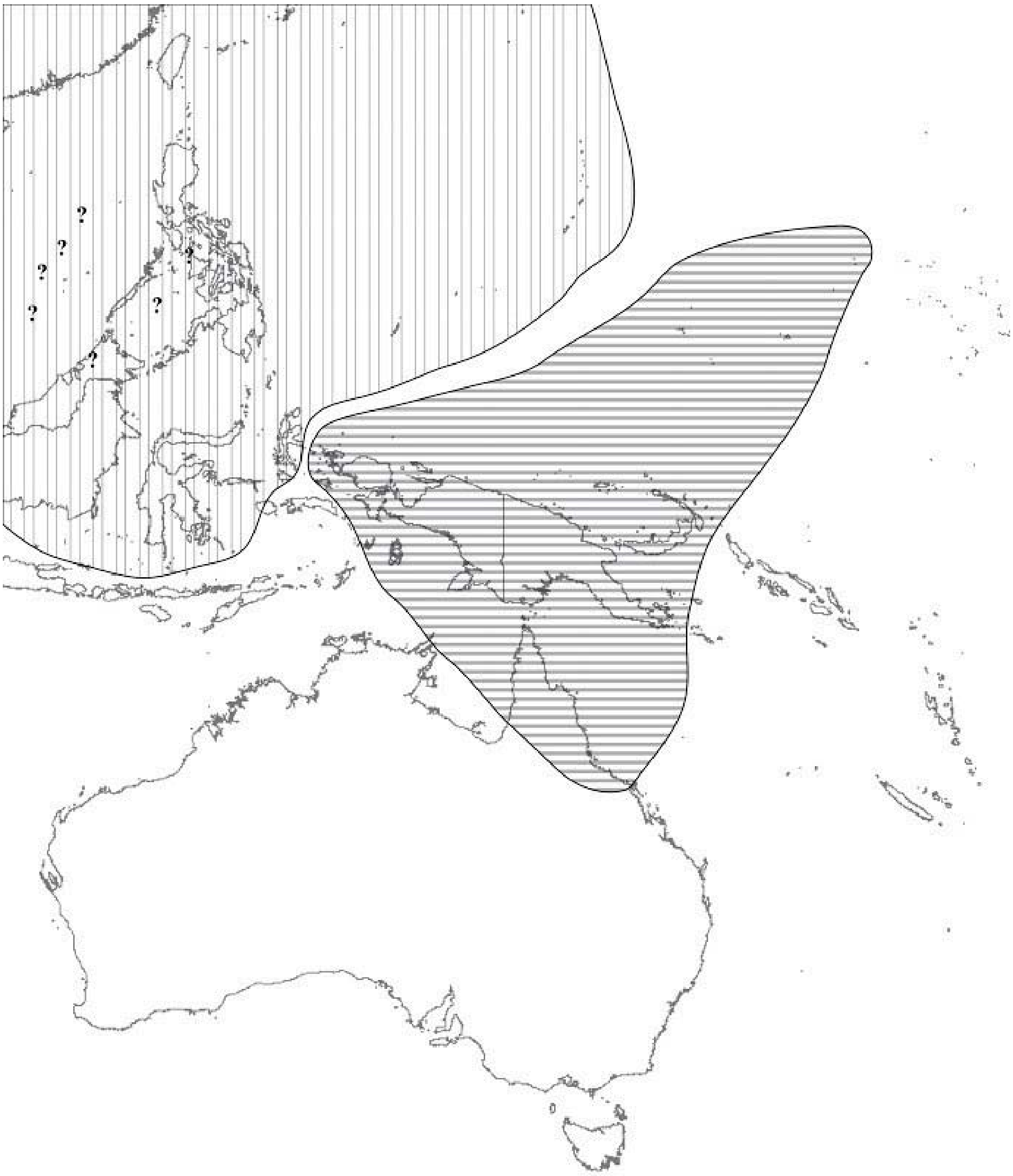

Figure 13. Distribution of two *Tramea transmarina* subspecies: *T. t. propinqua* (horizontal lines) and *T. t. euryale* (vertical lines).

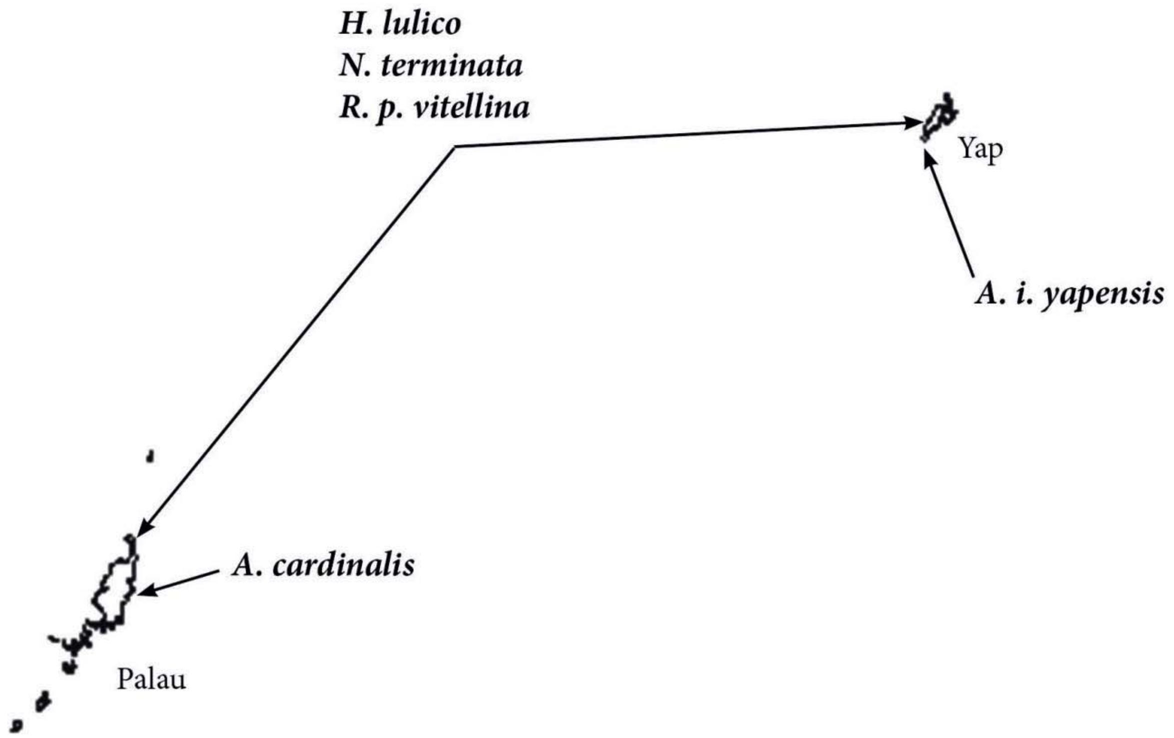

Figure 14. Distribution of *Agrionoptera* species in west Caroline Islands and other species shared between Palau and Yap: *Hemicordulia lulico* (endemic to both islands), *Neurothemis terminata* (occurring also in SE Asia), *Rhyothemis phyllis vitellina* (occurring also in Guam, Mariana Islands).

Figure 15. Distribution of *Lathrecista asiatica* subspecies within the Pacific area: *L. a. festa* (solid circles), *L. a. asiatica* (open circles), a possible new subspecies (dashed lines). Question mark is given for the populations inhabiting Vanuatu as their status has not been assessed yet.

erico confined to Kosrae and *H. haluco* to Pohnpei, while the younger islands of Yap and Palau share another endemic, *H. lulico*. No *Hemicordulia* was reported on Chuuk which is situated between those islands (Fig. 12).

Endemism at lower taxonomic level is even more striking. *Tramea transmarina propinqua* Lieftinck, 1942 (Fig. 13) is reported over a large range extending from Australia through the Marshall Islands to Chuuk Island (Lieftinck 1962; Paulson & Buden 2003). West Caroline Islands and Mariana Islands are inhabited by *T. t. euryale* Selys, 1878 (Lieftinck 1962; Buden & Paulson 2007). Assuming this information is accurate, it is unclear how the two wide-ranging subspecies differentiated and are maintained in such powerful fliers as *Tramea*.

Asahina (1940) was surprised that Palau and Yap (Fig. 14) share many common species such as *H. lulico*; *Neurothemis terminata* Ris, 1911; *Rhyothemis phyllis vitellina* Brauer, 1868. Yet in *Agrionoptera* Brauer, 1864 both islands have different species. Lieftinck (1962) assigned Palau specimens to *A. cardinalis* n. sp. and Yap specimens to *A. i. yapensis* n. subsp. *Agrionoptera* extends from India through SE Asia to the Pacific (Theischinger & Hawking 2006).

Marinov et al. (in prep./a) reported on an atypically small form of *L. asiatica* inhabiting the Samoan archipelago (Fig. 15). It not only differs by body size, but has unique morphological features on the head and thorax which will probably support a subspecies rank in a more detailed study. Specimens with these characteristics were observed throughout the whole archipelago from Savai'i to Ofu (Manu'a group) and for the moment the form is considered unique to Samoa. So far two subspecies have been described: *L. asiatica festa* Selys, 1879 (Australia, New Guinea, New Caledonia, Solomon Islands) and *L. a. asiatica* (Fabricius, 1798) (Fiji, Tonga, and Samoa; Samoan populations require revision).

2. Lack of certain families. Several families, including Calopterygidae, Lestidae and Gomphidae, are otherwise distributed worldwide, but are absent from or barely enter the Pacific islands. Not all of these are powerful fliers, but if they have dispersed from a centre of origin then they were very successful in occupying enormous parts of land and overcoming transoceanic barriers. So it is unclear why such powerful fliers as Gomphidae, which supposedly invaded nearly the entire globe by crossing the Atlantic and Indian oceans, stopped dispersing at the margin of the Pacific. It should be much easier for gomphids to fly from Indonesia via New Guinea to the Solomon Islands and continue further into the Pacific than to cross between Europe and North America, for example. The Pacific Ocean offers a wide array of islands of various dimensions which would be easy enough to conquer if the power of dispersal really did exist to the levels that have been proposed for the Pacific Odonata. Moreover, Lieftinck (1968) considers the occurrence of *Ictinogomphus australis* (Selys, 1873) on Rennell Island, Solomon Islands is evidence of its great dispersal potential. However, its range stops there and does not continue further in the Pacific, which is difficult to explain in a dispersal model.

   Calopterygidae are found worldwide except in Australia, southern South America and Antarctica (Kalkman & Orr 2013). Five species and subspecies are known from New Guinea and its satellites (Michalski 2012), but the family is not known from any of the Pacific islands east of New Britain (Marinov & Pikacha 2013) (Fig. 16).

Lestidae are represented with at least 14 species in Australia (Theischinger & Hawking 2006) and 10 species in New Guinea (Kalkman & Orr 2013), but their number gradually decreases from New Guinea east/south-eastwards – two species in New Caledonia, one in Vanuatu, one in Fiji and one in New Zealand (Fig. 17).

Gomphidae are well represented in the Oriental region (Orr 2003) and Australia (Theischinger & Hawking 2006), but just one species (*Ictinogomphus australis lieftincki* Schmidt, 1935) occurs in New Guinea and this only extends as far east as the Solomon Islands (Fig. 18).

Families such as Isostictidae and Synthemistidae on the other hand are confined to the Australian and Papuan regions (Michalski 2012) with New Caledonia as their eastern most distribution point (Fig. 19).

3. Highly disjunct distribution. Disjunct areas in Pacific Odonata are observed at both genus and family level. Aerial dispersal is unlikely to create disjunct areas or what is termed here “selective distribution” (see next point), transporting species for thousands of kilometres without leaving populations on archipelagos in between.

   Teinobasis fatakula Marinov & Donnelly 2013 for example for the moment is only found on the small island of ‘Eua, Kingdom of Tonga where it occupies an area of just 4.5km^2 (Marinov & Donnelly 2013). Its closest relatives live nearly 3,000km NW in the Solomon Islands (Fig. 20). There is also a gap in *Teinobasis* in the Caroline Islands. Buden & Paulson (2007) record the genus on Palau, Pohnpei and Kosrae, but not on Yap and Chuuk (Fig. 21). They explain this situation with the low relief and the paucity of stream habitats. However, *T. fatakula* on ‘Eua Island survives in much more extreme environmental conditions.

   The Australian (*Petalura* Leach, 1815) and New Zealand (*Uropetala* Selys, 1858) members of family Petaluridae have their relatives in other parts of the Pacific margin, in Chile (*Phenes* Rambur, 1842), Japan (*Tanypteryx* Kennedy, 1917) and the west coast of North America (*Tanypteryx* Uhler in Selys, 1859), with no any representative in between (Fig. 22). *Tachopteryx* Uhler in Selys, 1859 inhabits the eastern coast of North America.

4. “Selective distribution”. Random aerial transport would tend to carry insects across the ocean, populating islands more or less equally, especially with widespread species that are the most likely colonists. This is especially applicable for the most remote islands. Highly dispersive taxa are supposed to arrive at very distant islands through a single dispersal event, because the probability of a single successful colonisation is greater than the combined probabilities of two consecutive shorter dispersal events (Crisp et al. 2011). However, some Pacific Odonata genera show similar distribution patterns, which seems to contradict random aerial dispersal.

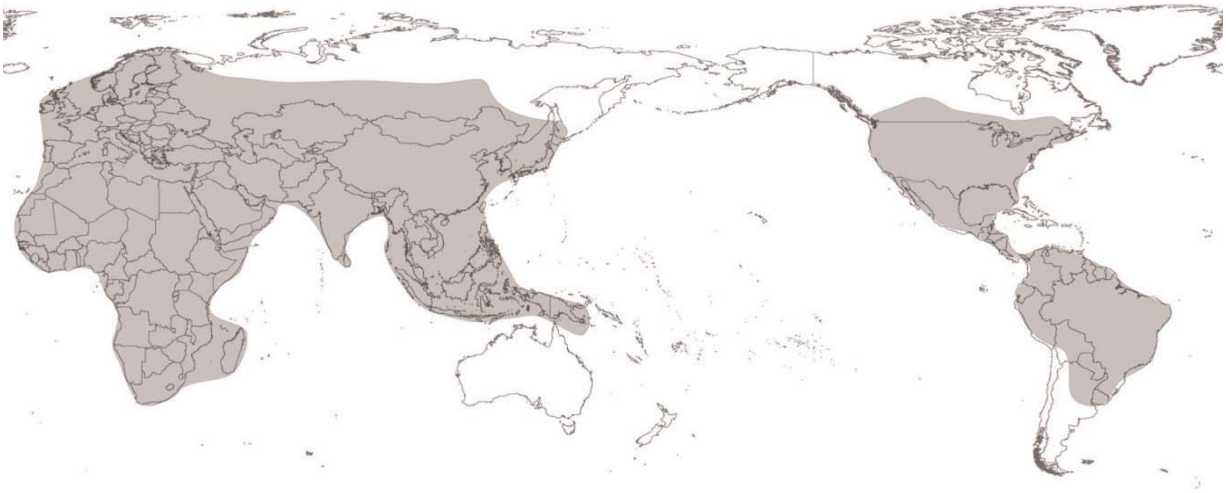

Figure 16. World distribution of Calopterygidae.

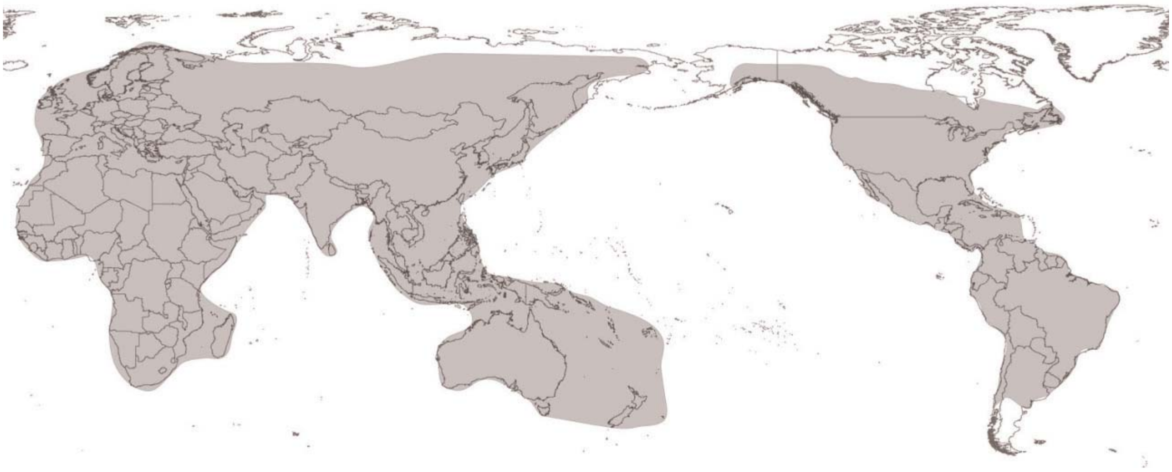

Figure 17. World distribution of Lestidae.

Figure 18. World distribution of Gomphidae.

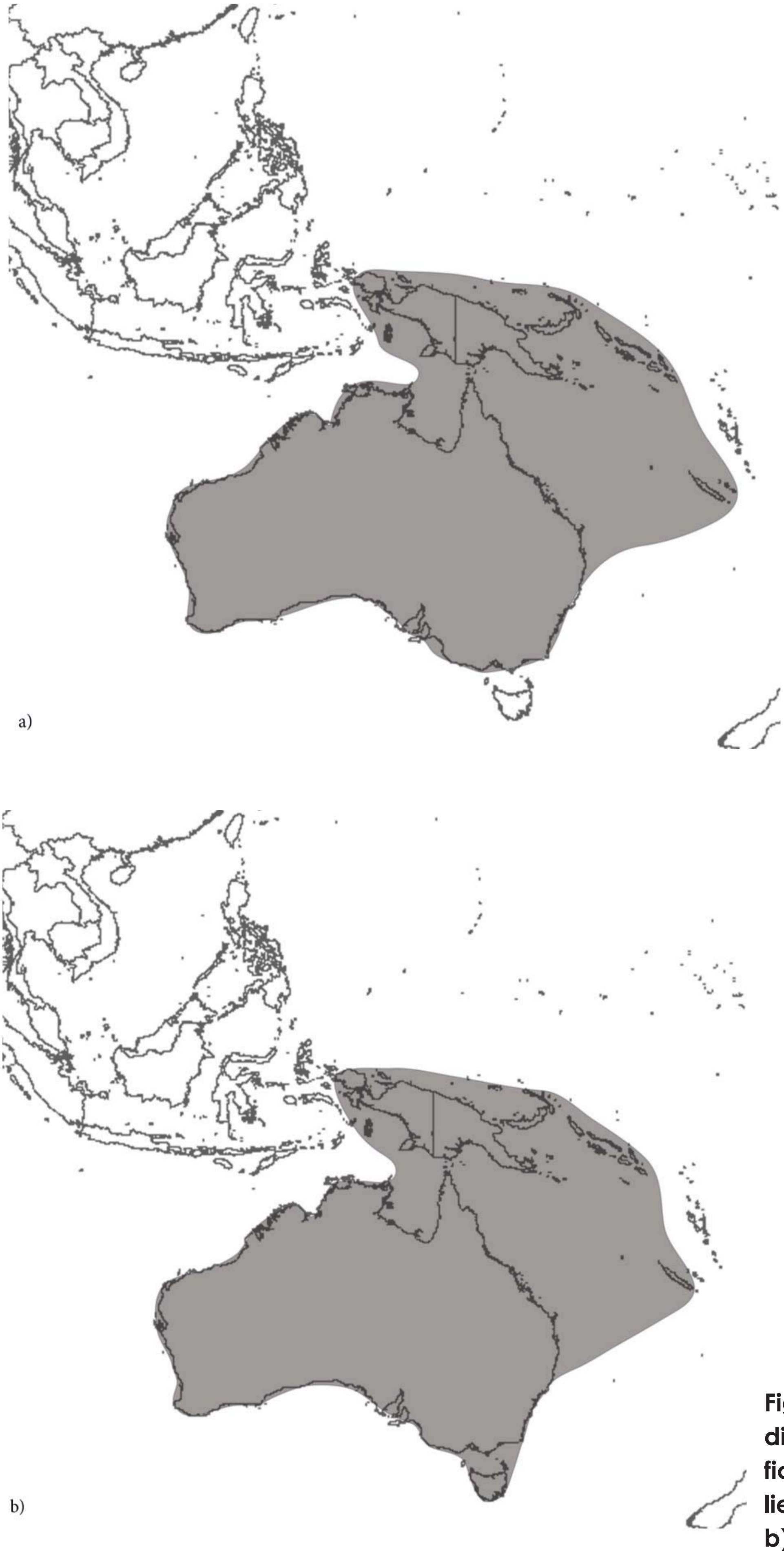

Figure 19. World distribution of Pacific endemic families: a) Isostictidae; b) Synthemistidae.

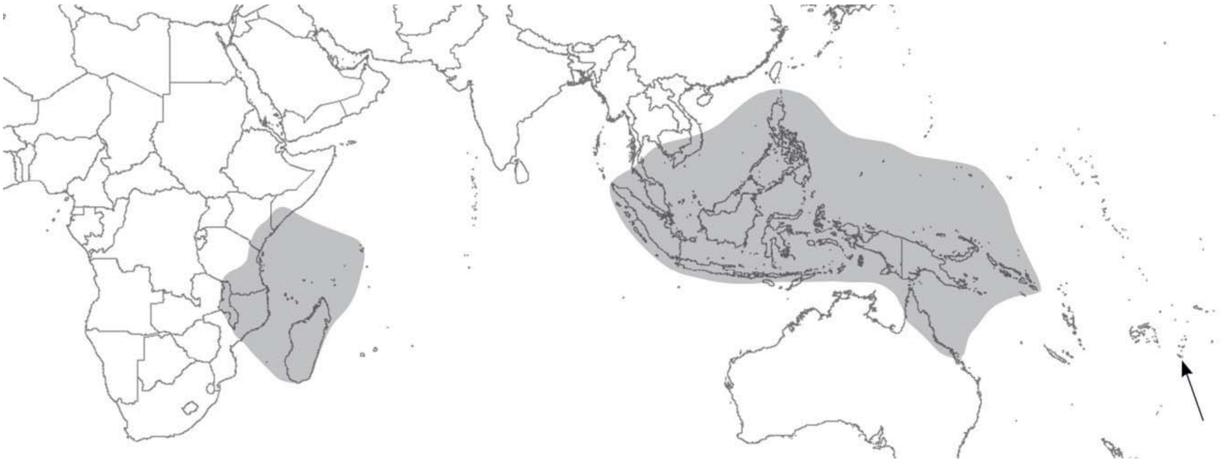

Figure 20. World distribution of *Teinobasis*. Arrow points to an isolated population endemic to 'Eua Island, Tonga.

Figure 21. Distribution of *Teinobasis* within the Caroline Islands. Arrows point to established populations only.

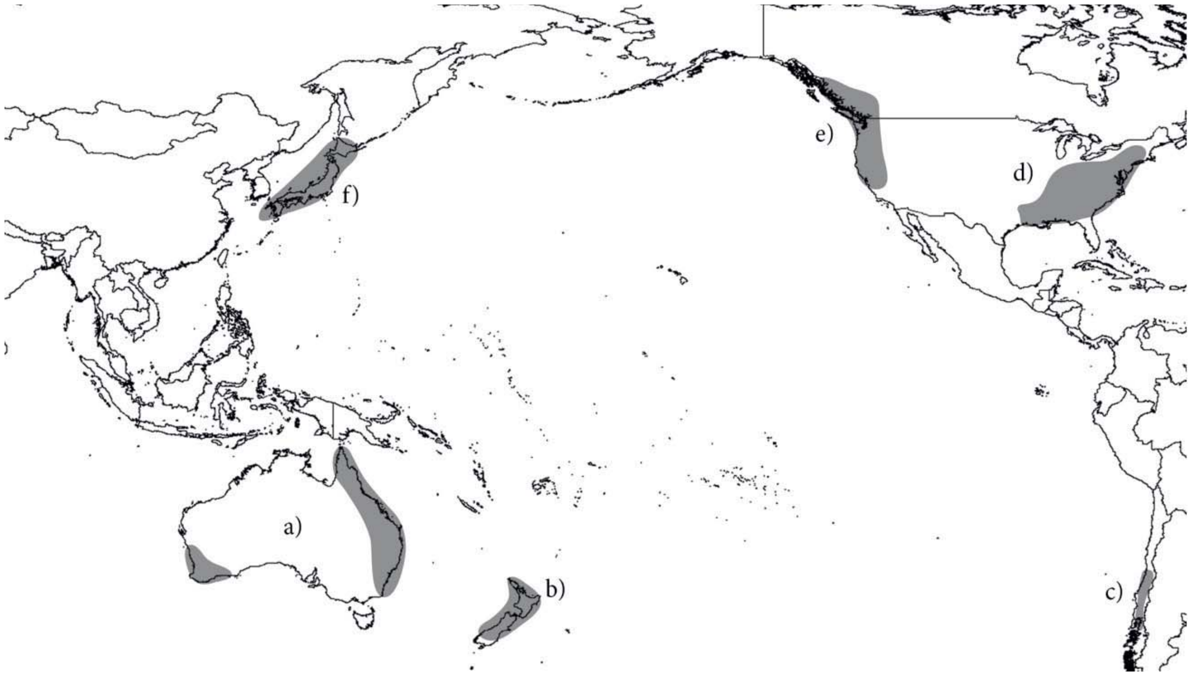

Figure 22. World distribution of Petaluridae: (a) *Petalura* (Australia), (b) *Uropetala* (New Zealand), (c) *Phenes* (Chile), (d) *Tachopteryx* (North America – east coast), (e) *Tanypteryx* (North America – west coast), (f) *Tanypteryx* (Japan).

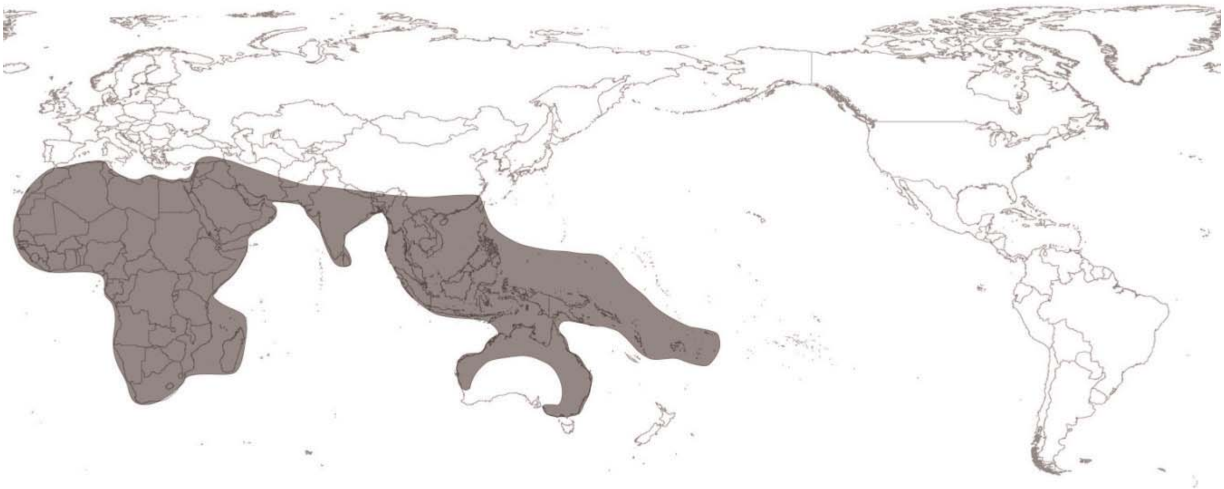

Figure 23. World distribution of *Pseudagrion*.

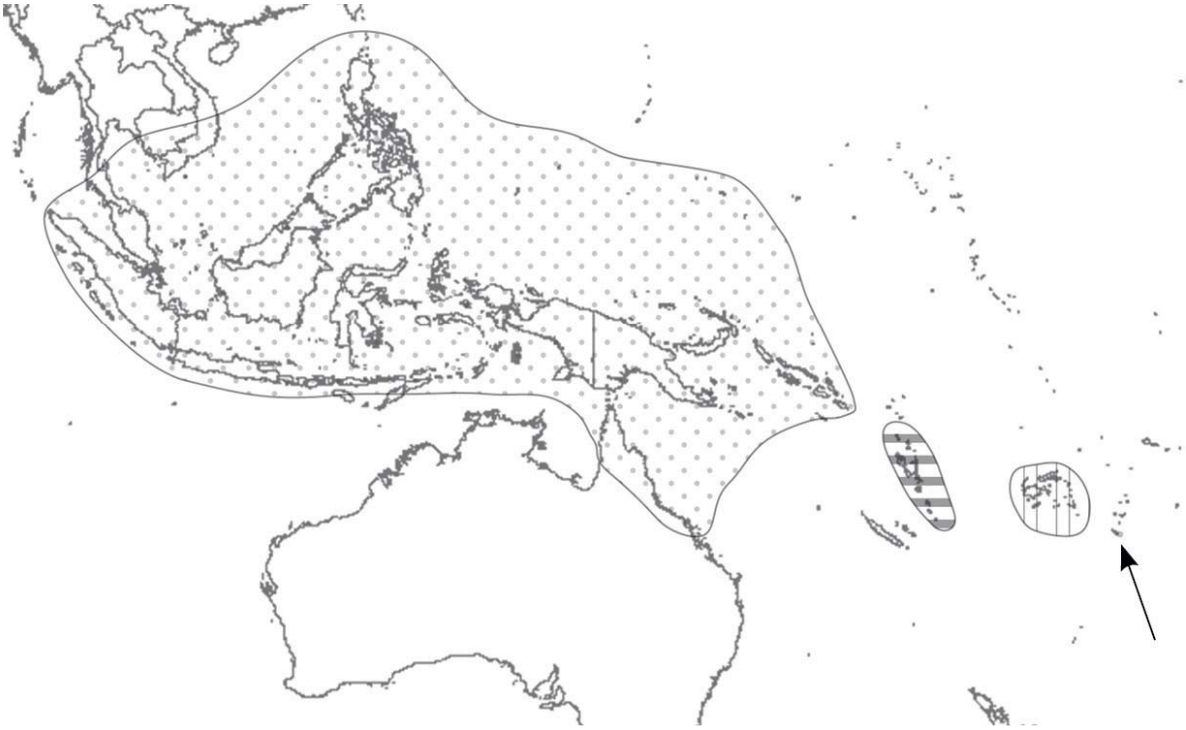

Figure 24. Distribution of the Pacific genera: *Teinobasis* (solid circles), *Vanuatubasis* (horizontal bars), *Nesobasis* (vertical lines). Arrow points to an isolated *Teinobasis* population endemic to ‘Eua Island, Tonga.

Figure 25. World distribution of *Procordulia* with focus on the Pacific region.

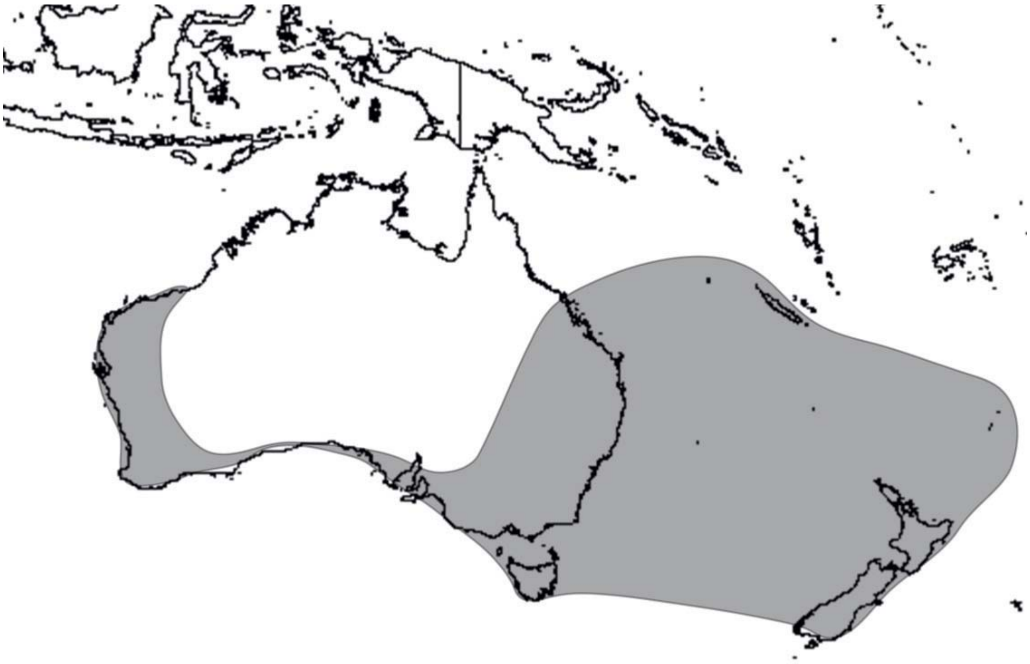

Figure 26. World distribution of *Aeshna brevistyla.*

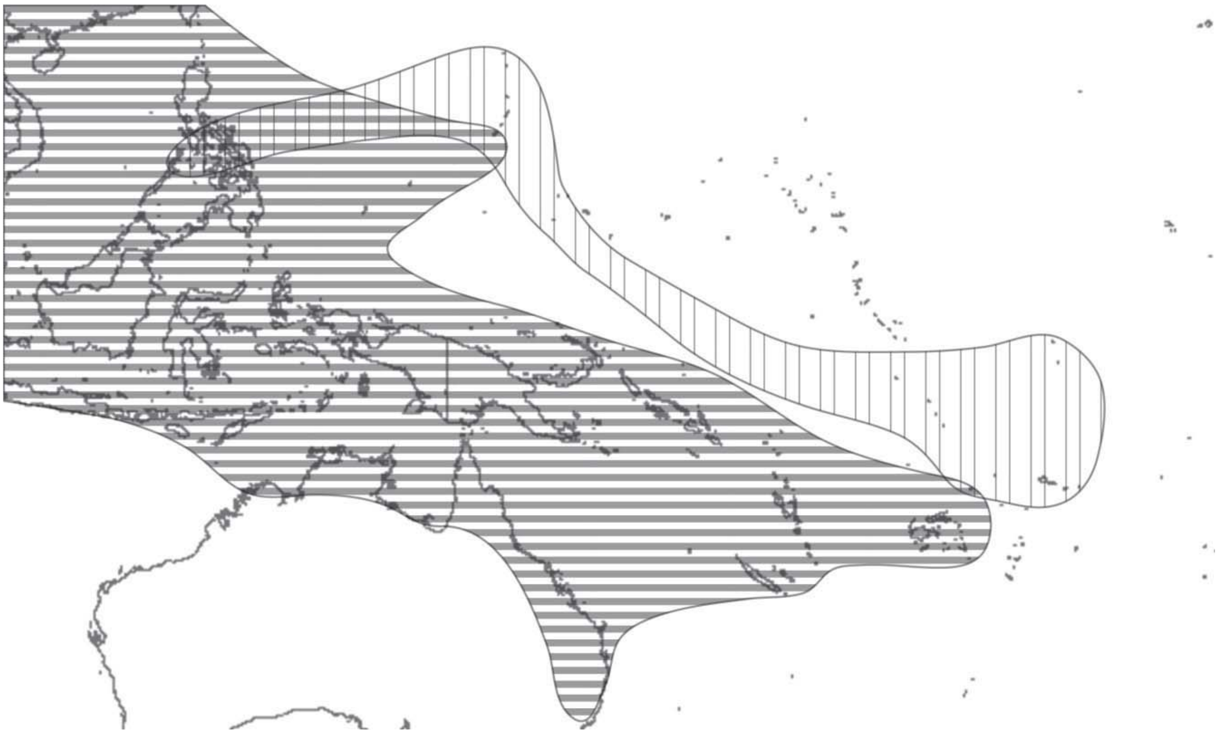

Figure 27. Distribution in the Pacific of: *Rhyothemis phyllis* (horizontal bars) and *Rhyothemis regia* (vertical lines).

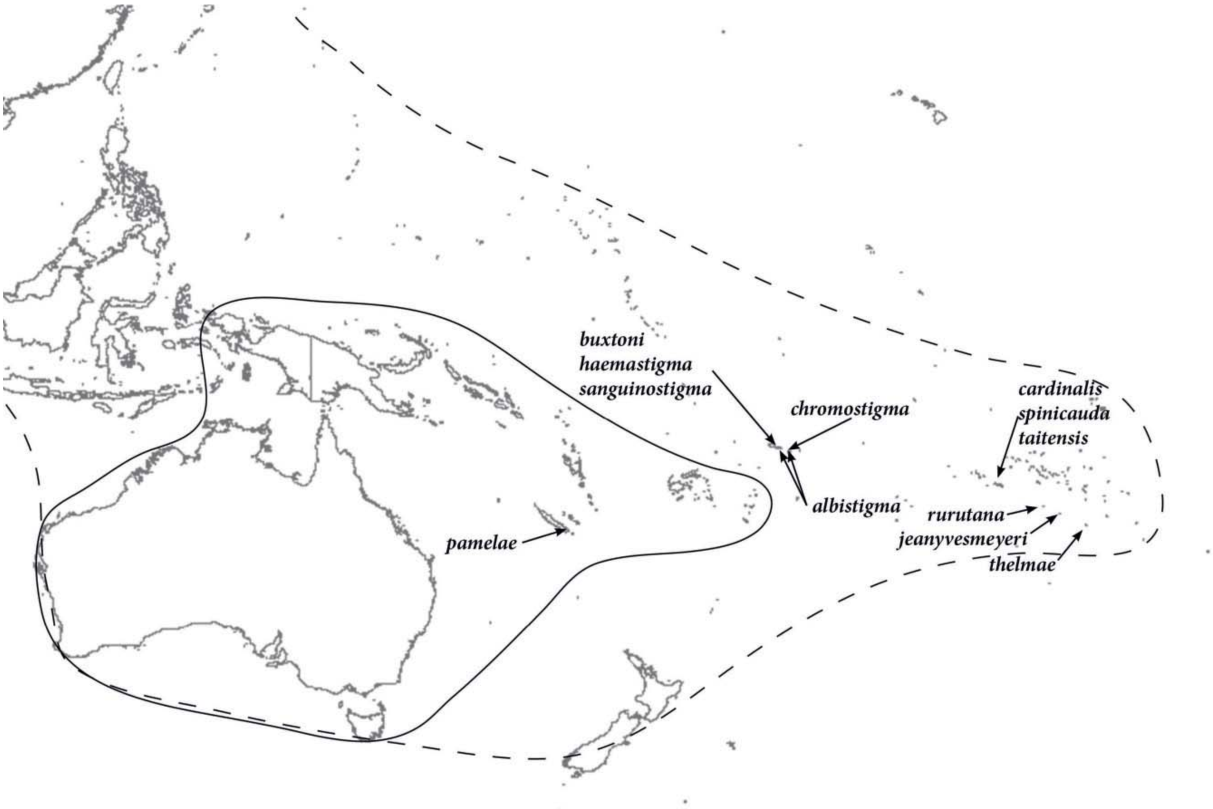

Figure 28. Distribution of *Ischnura* spp. within the Pacific. Arrows point to the areas of distribution of the endemic species. Two wide spread are indicated: *I. aurora* (dashed line) and *I. heterosticta* (solid line).

Pseudagrion with 146 described species is one of the most speciose dragonfly genera (Schorr & Paulson 2015), and it is distributed all over Africa, Middle East, India, AE Asia to Micronesia and Australia. In the Pacific it is represented with single species/subspecies in Vanuatu, Samoa, Fiji and Tonga, but no species are reported from New Caledonia, Norfolk Island or New Zealand (Fig. 23). *Pseudagrion* species inhabit both lentic and lotic waters. It is possible that all Pacific representatives are descendants of *P. microcephalum* (Polhemus et al. 2000) which although found along canals and rivers (Subramanian 2009) is commonly found in lakes, drains and lily ponds (Orr 2005). The overall paucity of wetlands in the Pacific islands is a likely reason for the scarcity of *Pseudagrion* in the region. Lotic waters on the other hand are very well represented, and so are the odonates associated with them. However, a complex of similar (possibly phylogenetically closely related) Coenagrionidae genera *Teinobasis*, *Nesobasis* and *Vanuatubasis* (including *Lieftinckia* from Platycnemididae) shows an interesting absence from New Caledonia and New Zealand, while reaching as far as Tonga (Fig. 24).

Procordulia Martin, 1907 on the other hand reaches New Zealand and is also spread in Australia, New Guinea, Philippines and SE Asia (van Tol 1997), but has no representatives on Solomon Islands, New Caledonia and Micronesia and does not continue further east from Fiji (Fig. 25).

A. brevistyla is distributed in Australia, New Zealand, and New Caledonia as well as the smaller islands of Norfolk, Lord Howe, and the Kermadecs, but it has not crossed the very narrow Torres Strait (Fig. 26). Belyshev & Haritonov (1983) pointed out that this otherwise cosmopolitan genus absences from New Guinea.

Rhyothemis is well-known for its wide distribution, which extends from Africa to the western Pacific (Theischinger & Hawking 2006). Figure 27 represents current knowledge on the species/subspecies distributions. It seems strange that *R. phyllis* has spread out over a very large territory, but has not advanced further east than Fiji and Wallis & Futuna. In Caroline Islands it occupies the western part (Palau and Yap), but not the eastern (Chuuk, Pohnpei and Kosrae). In Mariana Islands it is confined to Guam Island. *R. regia* on the other hand extends from the Mariana Islands to Samoa. While *R. phyllis* has developed endemic subspecies for the entire region, *R. regia* is represented with just one subspecies throughout. Both species co-occur only in Kikila Lake, Wallis Island (Papazian et al. 2007).

5. Inverted taxonomic ratio. The European and North American Odonata yield about twice as many Anisoptera species as Zygoptera (Dijkstra & Lewington 2006, Paulson & Dunkle 2012). Two Pacific island groups, Fiji and Hawaii, are perhaps the only two areas in the world where the ratio is instead about 2:1 and 4:1 respectively in favour of Zygoptera (Marinov et al. in prep./b). Samoa approaches these figures, but its fauna is too poorly studied to allow any further conclusions. The inverted taxonomic ratio in favour of Zygoptera over Anisoptera does seem to support the hypothesis of aerial dispersal for colonisation of the Pacific islands. Zygoptera are smaller bodied than Anisoptera, and weaker

fliers. Zygoptera were probably more vulnerable to passive transport by air currents between islands. If so, then a phylogeny of the Pacific taxa will reveal eastern groups to be nested in groups further west. French Polynesian *Ischnura* for example should be nested within the Samoan complex of species and so forth going westwards towards Australia and New Guinea. Presently we do not have evidence either way, but with the current state of knowledge such "nestedness" seems improbable. Society and Austral Islands together (Fig. 28) have six endemic *Ischnura* (*cardinalis* Kimmins, 1929; *jeanyvesmeyeri* Englund & Polhemus, 2010; *rurutana* Englund & Polhemus, 2010; *spinicauda* Brauer, 1865; *taitensis* Selys, 1876; *thelmae* Lieftinck, 1966), and both West and American Samoa share five endemics (*albistigma* Fraser, 1927; *buxtoni* Fraser, 1927; *chromostigma* Fraser, 1927; *haemastigma* Fraser, 1927; *sanguinostigma* Fraser, 1953). Further west to the Solomon Islands and Micronesia only New Caledonia has one endemic species *I. pamelae* Vick & Davies, 1988. All other island groups have one of the two (or both of them) widely distributed *I. aurora* and *I. heterosticta* (Burmeister, 1839).

6. Species diversity does not regularly decrease from West to East. Decreased species diversity is a phenomenon that is usually explained with the increased distance of the islands from the supposed main source populations (Keppel et al. 2009). The long distance from the perceived source population on SE Asia was used by Buden & Paulson (2003) and Buden (2008) to explain the very depauperate fauna of Kosrae and Nauru, in accordance with the MacArthur & Wilson (1967) model of island biogeography. Heads (2012) suggested an alternative view that explains the same phenomenon with the decreased surface area of the islands from West to East. Figure 29 displays the Odonata species number per archipelago taken as a geographic unit and not as individual islands within the group. This is a preliminary study and further interpretation of the results seems premature before more faunistic and taxonomic work is carried out. The Solomon Islands, for example, have a very large total surface area and although are considered one of the best studied archipelagos (Marinov et al. in prep./b) there are still large underexplored areas on many isolated islands there that will definitely increase the total species number in future studies. In the small territories of Cook Islands and Marshall Islands it is unclear if local species have populated those islands by their own dispersal abilities or were brought by humans. However, even at this stage there are certain distribution patterns that are unlikely to change considerably in future studies. New Zealand, New Caledonia and Fiji are the best-studied Pacific archipelagos in terms of their Odonata fauna (Fig. 30). Fiji is the eastern most of the three and has a total surface area almost identical to New Caledonia, but has the largest species number of any other Pacific archipelago – nearly 80 including discovered, but undescribed species. For other islands, the numbers of species may appear small, but they are related to the island area and distance from the equator. Pohnpei, for example has only 15 species, which is the number known for the whole territory of New Zealand, and these species live on an area of only 336 km^2. There is little historical evidence for changes of distribution in the species in

the past, however, with at least eight endemic species (Paulson & Buden 2003) on such a small territory the species richness is remarkably high. In fact the species number is almost twice as high as the species established in Chuuk Island which is situated more than 700 km to west and is closer to the mainland of Asia, but is half the size of Pohnpei.

In general species diversity does seem to decrease towards the far eastern end of the study area, with Easter Island having just one dragonfly species – *P. flavescens*. The depauperate fauna of the Easter Island has been attributed to the small size, isolation and young age of the island (Dumont 2002) and to introduced mosquito fish (Dumont & Verschuren 1991).

7. Absence of wide spread species from some regions. As with "selective distribution", some widespread species "avoid" particular islands or have not yet been recorded there. It seems strange that such a common species as *P. flavescens* was not recorded during some odonatological studies although they were searched for specifically. It was absent from Ofu Island although the whole length of the island was walked in a search for that species after recording four others from the only wetland on inland (Marinov et al. in prep./a). The apparent absence of *P. flavescens* on Ant atoll was recorded as

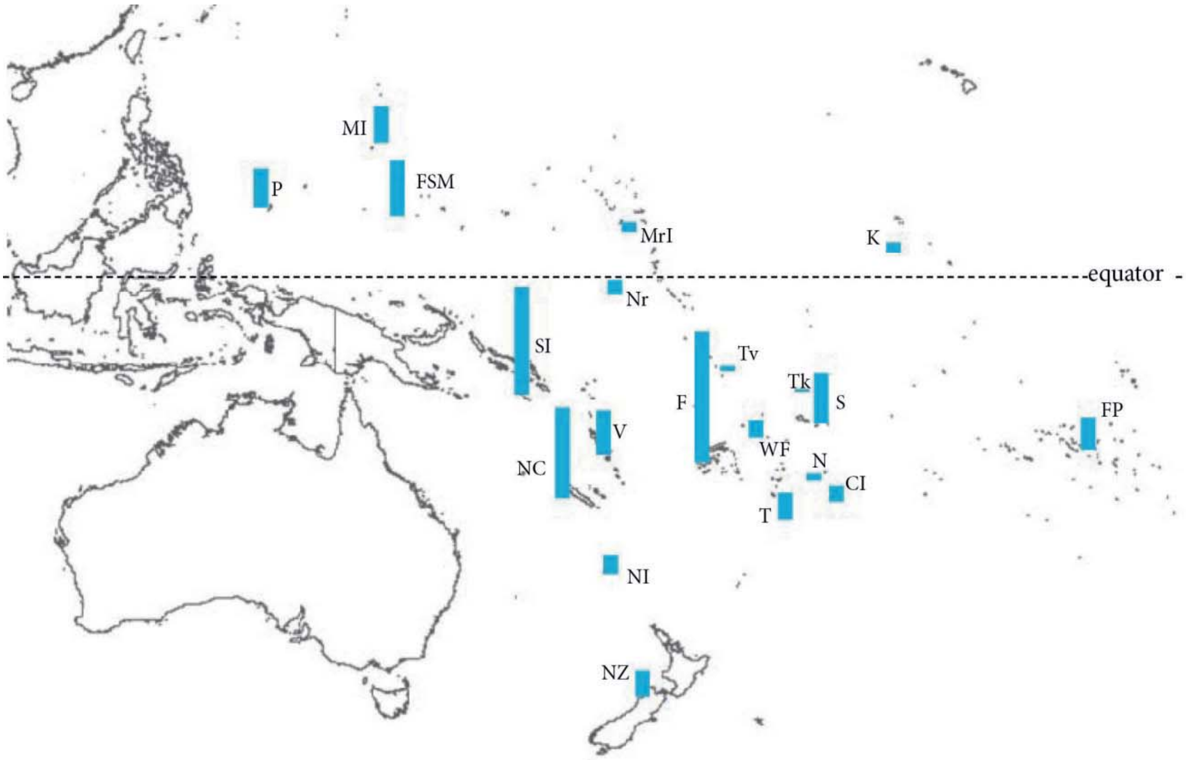

Figure 29. Species richness of the Pacific Odonata taxa. Blue bars equal species number per archipelago. Abbreviations: CI – Cook Islands, F – Fiji, FP – French Polynesia, FSM – Federal States of Micronesia, K – Kiribati, MI – Mariana Islands, MrI – Marshall Islands, N – Niue, NC – New Caledonia, NI – Norfolk Island, NZ – New Zealand, Nr – Nauru, P – Palau, SI – Solomon Islands, S – Samoa, T – Tonga, Tk – Tokelau, Tv – Tuvalu, V – Vanuatu,WF – Wallis & Futuna.

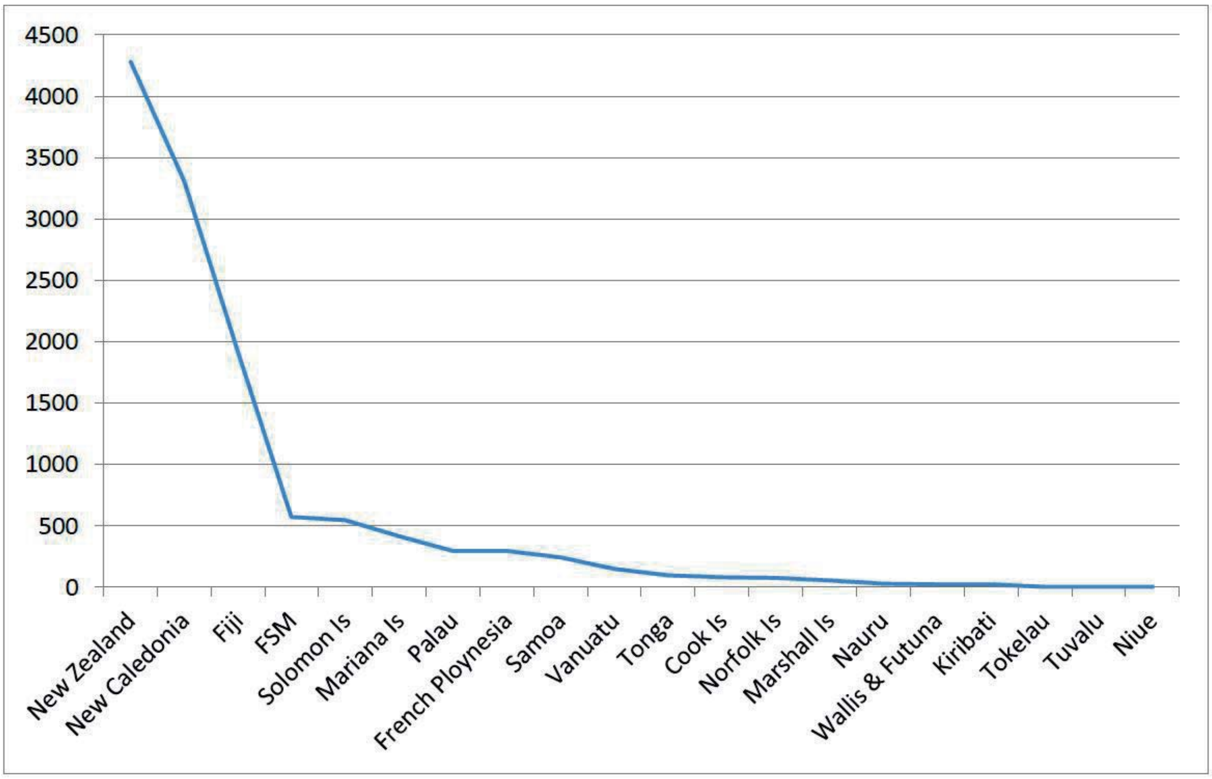

Figure 30. Pacific Odonata studies given as records per archipelago.

a greater anomaly (Buden 2004). Evenhuis et al. (2010) commented that a: “... conspicuous absence on Pagan is the widespread and long-distance flier, *P. flavescens*”. As mentioned above, the same species has recently arrived on Norfolk Island (Endersby 2002). It has frequently been observed in New Zealand too, but the earliest record dates back only to 1950 (Rowe 1980). As with the example from Norfolk Island, it is surprising that no one has recorded it before the 1950s. While the climate of New Zealand is considered unfavourable for establishing breeding populations of dragonflies (Rowe 1987), Norfolk Island should be fairly easy place to colonise having in mind that the species occurs further south on the Kermadec Islands (Rowe 1980).

Pacific Odonata biogeography revisited

The biogeography of Pacific Odonata cannot be explained only by dispersal and the wind patterns across the region. The distribution of species, genera and families does not seem to be random. A new approach is needed to tackle the problem and propose an explanation that seems more plausible in the light of the seven “oddities” given above. A new approach would explain the seven phenomena by the composite influence of vicariance, dispersal within the ecological capacity of species and human mediated transport. Unfortunately this new approach can only suggest possible avenues for research, but with the present state of knowledge, it cannot answer every question about the group. Figure 30 compares the data per Pacific archipelago either as published records or personal observations. Lieftinck (1949b) thought of Odonata of the Solomon Islands as the most neglected of the entire Pacific, however, according to the classification given here, Solomon Islands ranks fifth. This is still a high position, but because of its large total surface area, the archipelago surely harbours many unknown species. Apart from New Zealand, New Caledonia and to some extent Fiji, other archipelagos still need odonatological revisions, despite recent sampling in Tonga, Samoa and French Polynesia. More intensive year round field work needs to be carried out in these regions.

The new approach suggested here calls for greater attention to geographical processes and influence of man in shaping the recent species distribution. Earlier views of Tillyard and Fraser were somehow forgotten, probably because of the strong opinions of Lieftinck who was one of the most influential authorities on Odonata in the twentieth century. Lieftinck accepted aerial, trans-oceanic dispersal as a means for Odonata populating oceanic islands, even for taxa such as *Eusynthemis*, that are otherwise known as habitat specialist which do not move away from their preferred environments.

Reviewing the extant Odonata taxa, there is an interesting distribution pattern at family level that could be attributed to the geological age of the taxa. Endemism at family level appears to be restricted to Zealandia. New Zealand is the eastern limit of the ancient Odonata family, Petaluridae. Ancient families such as Argiolestidae, Synthemistidae and Isostictidae extend as far east as New Caledonia, while young families such as Coenagrionidae and Libellulidae are very poorly represented on New Caledonia (Davies 2002). Collectively these two families form only 42% of the fauna of New Caledonia, while further east they are totally dominant with about 92% of the fauna of Fiji, 75% of Vanuatu, 77% of Samoa, 82% of Tonga, 78% of Cook Islands plus Niue, 64% of Society Islands, 70% of Austral Islands and 75% of Marquesas Islands. The remaining percentages for those archipelagos are made up of Lestidae, Aeshnidae and Corduliidae.

Lestoidea are known from early Cretaceous (Greenwalt & Bechly 2014), but crown Lestidae have a minimum age of 29.2 Ma (Nel & Paicheler 1994). The family extends east to Vanuatu, Fiji and New Zealand with just a single species found in all three places.

Aeshnoptera are of Jurassic origin, but Aeshnidae s.s. are younger, Cretaceous (Bechly et al. 2001) with minimum age for clade 139.8 Ma (Pritykina 1977). Three species are widely distributed in the Pacific reaching east to Samoa and some continuing east to French Polynesia.

Corduliidae is a monophyletic family close to Libellulidae (Ware et al. 2007) and although libelluloids were established in the early Cretaceous (Huang and Nel 2007; Nel and Huang 2015) the minimum age for crown Corduliidae is estimated at 12.7 Ma (Kiauta 1969). They are represented in the Pacific with two to three species per archipelago with one of them wide spread and the others are endemic.

It seems peculiar that lines coinciding with Tonga Trench and Mariana Trench act as a kind of barrier for the spread of ancient families east into the Pacific and limit the distribution of some taxa. The Tonga trench boundary is passed by some Aeshnidae (*Anaciaeschna*, *Gynacantha* and *Anax*), which are all of younger age (von Ellenrieder 2002), while the Mariana trench is the border between distribution areas of several taxa at species and lower level, such as the Caroline Islands endemic *Hemicordulia* and *T. t. transmarina-T. t. euryale*. The new approach to the Pacific Odonata biogeography proposed here works with the assumption that although they can potentially disperse, it is unlikely that Odonata have occupied the whole of the study area relying on their own flight and the support of wind circulation. Oceanic distances of hundreds of kilometres are too much of a barrier for a successful dispersal. They may be overcome by single individuals, but those should not be considered as highly dispersive by the definition given above. Without further immigrants, accidental individuals reaching new territories are unlikely to establish viable populations that would survive and diversify to the extent seen in the Pacific Odonata.

A transport of much larger number of individuals, as well as time commensurable with geological, are required to provide the necessary *Ne* to avoid entering in a population bottleneck. Such transport may be provided with the movement of the oceanic plates. Either due to a land connections around the closed Pacific, with island arcs and now-submerged continental plateaus moving across the ocean, a large initial stock was probably transported or broken up by a number of geological events. In those situations, ancient taxa were probably more "reluctant" to occupy new places as they would have already become highly specialised to their existent environment. Younger taxa, usually those with wide distribution (Belyshev 1969), instead invaded new islands as the plates have moved across or broke apart.

A closed Pacific Ocean in the geological past would explain the disjunction of the ancient family Petaluridae. In the plate tectonic model the recent members of this family become very wide apart which would take an extreme dispersal power to cross the existing Panthalassa. The Expanding Earth model seems to fit better for this family as it forms evidence of the zipper effect proposed by McCarthy (2003). A spreading Pacific ocean could explain the existence of "continental rocks" and what Shields (1976) calls "...debris left from continental rifting ..." for the Pacific islands. Under this scenario disjunct areas of higher taxa are probably a consequence of the plate movement with old taxa remaining on the main land masses while younger ones spread out to new territories. The opening of the ocean would have restricted ancient Odonata families to what is now Zealandia. These islands were among the first isolated by seafloor spreading, and so they would have had enough time to develop the endemism that now exists to genus and family level. The geographical location and individual history of the Pacific archipelagos should be considered in future biogeographic reviews.

Naturally, transportation of organisms between islands does not necessarily occur in a short space of time, but over long periods of geological history it becomes more likely. Therefore, young taxa at the initial time have "grown up" to a particular age when they become sedentary to the islands where the initial stock has settled and speciated afterwards. Probably that is why closely related taxa such as *Teinobasis*, *Nesobasis* and *Vanuatubasis* did not advance further than Tonga. Islands such as New Zealand and New Caledonia were probably already isolated as part of Zealandia by the time of major geological processes affecting other regions of the Pacific. For example diversification of Coenagrionidae and *Pseudagrion* in particular may have postdated the disconnection of New Caledonia-New Zealand from other parts. *Pseudagrion* is probably a young genus with endemism in the Pacific only at subspecific level. The close relationship between *Pseudagrion* and the Hawaiian *Megalagrion* McLachlan, 1883 has to be considered also. This led to the suggestion of dispersal into Hawaii from the west (Jordan et al. 2003), which is opposite to the general view that the Hawaiian islands have been colonised from the east (Gillespie et al. 2012). Under the view proposed here, a western relation of the Hawaiian group is more probable, and this is also indicated by the phylogenetic analyses presented by Polhemus (1997) and Jordan et al. (2003). Nevertheless, the mechanism of transportation to the Hawaiian islands did not have to be by wind. Another possibility is plate tectonics events similar to those that Grehan (2001) suggested for the origin of the Galapagos biota. The formation of the "Sorachi Plateau" (Kimura et al. 1994), or a similar event, could explain the origin of Micronesian Odonata and the observed tendency of older islands at the east Caroline Islands to have more endemic species (Asahina 1940).

As young taxa with great potential for speciation, Coenagrionidae have possibly found good conditions to develop on larger islands such as those in Fiji. The diversification there is remarkable with *Nesobasis* (21 described species and at least another 10 pending descriptions) being one of the most speciose Odonata genera found in any oceanic island group in the world (Beatty et al. 2007). The situation is comparable only with Hawaiian *Megalagrion* (Jordan et al. 2003). These genera contribute significantly to the increased ratio in favour of Zygoptera over Anisoptera. Moreover, *Nesobasis* and *Melanesobasis* are both stream dwellers, as is *Teinobasis* and possibly their common ancestor.

Endemism in this scenario is a consequence of evolutionary processes acting in situ in individual islands and archipelagos. Most species that are now widespread may have been transported by man and are probably recent arrivals to those Pacific islands.

Lack of certain families, like Gomphidae and Calopterygidae could be explained by vicariance at the initial break up of Gondwana. These two families are almost exclusively stream dwellers. Along and east of the Australian-Papuan region they are replaced by Argiolestidae, Isostictidae and Syntemistidae (New Caledonia) with addition of Chlorocyphidae, Platycnemididae, Platystictidae, Protoneuridae (Solomon Islands). A possible relation exists between *Synthemis* and *Cordulegaster* Leach, 1815 and vicariance was proposed by Tillyard (1910) based on the analysis of the larvae.

Obviously it is not the distance from the source, but the size of the island and its geographic location especially latitude that are important in species diversification and to some extend abundance. ‘Eua Island in Tonga maintained *Teinobasis* species as the only member of the genus which did not evolve to higher taxonomic level probably because of the combined influence of: (1) small land area, (2) southern location for the genus, and/or (3) conservatism of its environment. Large islands such as New Zealand may appear impoverished, but one has to take into account the southern situation and geological history. At 25 Ma (Gibbs 2010) New Zealand was a low-lying archipelago where it is possible that only lentic Odonata species existed after the breakup of Gondwana. Lotic habitats may still have been represented, but were probably inhabited mostly by other insect groups. Uplift of the land and formation of the major mountain ranges in the North and South Islands have made conditions even worse for odonates restricting the available surface area for developing of lentic habitats or exposing the later to the extreme weather conditions of the mountain regions. Some *Xanthocnemis* trapped in what became mountain tarns on the South Island have started adapting to the harsh environment, but have not yet developed into new species (Amarya-Perila et al. 2014). Other individuals from the same genus have probably secondary entered shady streams in forests in the northern North Island and are also evolving new features, but have not differentiated from the wide spread *X. zealandica* (Marinov et al. in press).

Hypothesis testing and applications

Donnelly (2005) regarded oceanic islands as ”... magnificent places to test biological theories”. Biogeography is perhaps the area which explores islands most of other sciences. However, one has to consider Belyshev (1969) point of view that zoogeography must be based on detailed zoogeographical studies of the particular animal groups which could be very different in their biology, historical and ecological peculiarities. Constructing a general zoogeographical scheme – it’s a task for the future when there will be more details on the individual groups. Making preliminary zoogeographical statements may lead to absurd conclusions that may sound very convincing (Belyshev 1969).

Indeed with the Pacific Odonata fauna so inconsistently and insufficiently studied where taxonomy is not completed yet as well as in the lack of comparative phylogenetical research, biological, ecological information and no historical data, any attempt for now to propose a new biogeographic hypothesis must be considered only preliminary and encouraging for future wider study on the group. The view on the Odonata biogeography expressed here could be just another speculation although it provides more clarifications of the present day status as far as we understand it for now.

There are several points that cannot be explained with the view proposed here, or seem contentious. One example is the occurrence of representatives of such an ancient group like Aeshnoptera as far as French Polynesia, however the family Aeshnidae s.s. are younger (see above). Another possible explanation is that some species have a recent distribution associated with man. Lieftinck (1953a) received specimens of *A. jaspidea* collected by a Cook Islands resident who has seen them flying in a large number over the lagoons. As they are also crepuscular fliers, they may have been attracted to lights on departing vessels and been transported east in this way. Averill (1995) reported a large number of *Anax ephippiger* (Burmeister, 1839) hovering around the decks of a lighted ship when the moon was obscured, although this did not occur on cloudless nights. Other species attracted to the light were commented in Umar et al. (2012). Human transport by ships might also be true for other widespread species such as *I. aurora*, *A. exsudans*, *T. transmarina* and *D. bipunctata*, and it was suggested for *P. flavescens* on Easter Island (Dumont & Verschuren 1991). Lieftinck (1962) gives *I. aurora* as a chiefly insular and coastal species, but it also has isolated, montane habitats in Java and New Guinea. The subspecies of *I. aurora* have not been revised yet and no subspecies have been proposed for the entire study region. Lieftinck (1949a) described *I. a. viduata* from central-western New Guinea and Lieftinck (1959) claimed it was restricted to Baliem River basin. The nominate subspecies also occurs in New Guinea, but is distributed to the north. If *I. aurora* populations on the Pacific islands have lived in complete isolation, they are likely to have developed further subspecies and the species needs further study. Papazian et al. (2007) discovered that *I. aurora* was not homogeneous across its range and suggested the elevation of *I. aurora rubilio* Selys, 1876 to species rank for populations west of the Wallace Line. Dumont (2013) provided molecular evidence for this. However, in this molecular phylogeny of the genus Dumont (2013) found New Guinean specimens from Baliem River (presumably *I. a. viduata*) closer to conspecifics from South Australia than to other New Guinean *I. aurora*.

However, the human influence on odonate distribution seems to have been overestimated. There is no proof that this is the way odonates have dispersed. *Anax gibbosulus* Rambur, 1842, for example is usually given as inhabitant of higher-elevation areas (Donnelly 1986). In the related species *A. guttatus*, its crepuscular life style may be taken as a probable mechanism for the distribution, but it is unlikely to explain the occurrence of *A. gibbosulus* on the high country areas of New Caledonia and Samoa.

Rhyothemis has developed Pacific endemism to subspecific level only, which, having in mind its taxonomic affinity to Libellulidae, should be an indication of a comparatively young age. However, it occurs on all tropical islands, including those with ancient origins, such as the Solomon Islands and New Caledonia, but does not inhabit islands east of Samoa. In the Cook Islands, Niue and French Polynesia it is absent, which contradicts the supposed pattern relating the age of the islands to the age of the taxa. *Rhyothemis* has developed endemic subspecies on many island groups, and this cannot be explained by recent anthropogenic distribution. A possible explanation for the subspecific differentiation is ecological specialization. *Rhyothemis* is an obligate pond dweller and often prefers the shadow of trees (Marinov & Waqa-Sakiti 2013), while the other widespread members of Libellulidae (*D. bipunctata*, *P. flavescens*, *T. tillarga* and *T. transmarina*) have been observed occasionally along streams and rivers. Possibility the scarcity of the lentic habitats east of Samoa limits the distribution of *Rhythemis*. *Orthetrum* on the other hand is also reported from lotic habitats in Fiji and Samoa (Marinov 2011; Marinov et al. in prep./a), but as with *Rhyothemis* does not continue further east of Samoa.

Norfolk Island is another island that the new approach does not fit well. It is believed to be located in part of Zealandia, in which case one would expect to see endemic species there. However, all eight species reported are widely distributed. One possible explanation is in the geological history of the island. It is an erosional remnant of a number of local volcanic centres that erupted several times in the Pliocene (at 3.05-3.3 Ma; Abell & Falkland 1991). Although it lies on the Norfolk Ridge, part of Zealandia, the Norfolk Island area was submerged for most of the post Gondwana breakup history. It appeared recently above the sea with the Pliocene volcanism and its highest point, Mount Bates, reaches 318 m elevation (Abell & Falkland 1991). For the short period of its existence, the island has been populated with a low number of Odonata species, probably most of which were brought by man. This was inferred above for the recent arrival of widespread species such as *P. flavescens*.

The new approach proposed here for Odonata could be compared with biogeographic studies on other Pacific groups. Such a review is beyond the scope of the current study, however, Adamson (1939) provides some curious facts on the fauna of some of the most remote islands in the Pacific. In the Marquesas Islands fauna he emphasised the lack of ancient orders and families such as Ephemeroptera, Plecoptera and Carabidae. Another ancient family, Kalotermitidae, is thought to have been transported to the islands by human trade in timber, which is usually hard and dry and provides a suitable habitat.

For now, studies on Pacific Odonata should focus on comparative taxonomy and phylogeny as the most probable ways to establish the relations between the Pacific Odonata. However, the interpretation of the results must be done with caution. A close relation between widespread species could be taken as a proof of recent dispersal with or without constant gene exchange. This dispersal may still be supported by the wind, but could be associated with human activities in the Pacific. Insects may not always be detected when the ship arrives in a new port. Being trapped on board they would probably take off in the air frequently to “investigate” for any potential terrestrial ground. When detected they may leave the vessel long before it boards the port.

Heiser & Schmidt (2010) used an alternative biogeographic approach to test old hypotheses on the biogeography of the western Palearctic Odonata. Relying on a large set of species presence/absence data combined with genetic studies, the authors were able to prove statistically what earlier researchers had suggested for the faunal groups of the region and about the influence of climate on dragonfly distribution.

A similar approach is needed here not only for investigating the biogeography of Pacific Odonata, but for the preservation of the unique island fauna. Distribution data could be used for predicting phenology patterns (Bishop et al. 2013) which are important for planning conservation actions. Maes et al. (2005) illustrated the use of species richness predictive modelling for designation of conservation areas. In their modelling Bishop et al. (2013) achieved a positive outcome relying on least 6,500 data entry per year. This is achievable by a well-known species distribution on a local scale. Unfortunately, for now at least, accumulating this magnitude of data for the Pacific Odonata seems very unlikely.

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