Neat and clear: 700 species of crane flies (Diptera: Tipulomorpha) link southern South America and Australasia

G U I L H E R M E   C U N H A   R I B E I R O and A N D R É   E T E R O V I C

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Abstract. A biogeographical analysis of crane flies (Diptera, Tipulomorpha) in the southern hemisphere is used to test if their distribution patterns provide evidence of biogeographical homology (shared history) in the South Pacific. Crane fly distributions are interpreted in light of patterns of endemism and diversity and published phylogenetic studies. A panbiogeographical approach, assuming that repeating distribution patterns strongly suggest the existence of past connections between the areas (biogeographical homology), is used. A clear pattern is revealed in which crane fly taxa shared between southern South America, New Zealand and Australia are restricted to that region. Thirty genera and subgenera, together comprising about 700 species, occur in both South America and Australasia and only in these areas. This distribution defines the limits of the South Pacific Track, a standard biogeographical pattern displayed by many taxa, including the southern beeches (*Nothofagus*). Although the distribution of some taxa spans the entire track, others are present in parts of the areas only, forming a nested set of distributions. Within the surveyed genera and subgenera, all individual species are endemic to one single region or continent, suggesting vicariance as the main process behind crane fly disjunctions in this part of the world. The nested set of distribution patterns could be explained by extinctions in areas where taxa were present previously. Alternatively, it may indicate historical absences and the existence of a heterogeneous set of ancestral distributional ranges. 'Gondwanan' may not be the best term for the observed disjunctions, which should be labelled as trans-Pacific instead. Recent molecular estimates of divergence times suggest a Permian origin of the earliest extant Diptera lineages such as the Tipulomorpha, followed by fast radiation in the Triassic. Although the differentiation of some crane fly groups occurring in the region may have been driven by recent Mesozoic and Cenozoic events of continental breakup, as least part of the fauna may have evolved allopatrically in response to older events. This may explain the overlapping distribution of subgenera in large genera such as *Gynoplistia*.

Introduction

The crane flies (suborder Tipulomorpha sensu Amorim & Yeates, 2006) include four common families of Diptera, the Limoniidae, Tipulidae, Pediciidae and Cylindrotomidae. The

group is worldwide and includes more than 500 genera and subgenera and over 15 000 species (De Jong *et al.*, 2008; Oosterbroek, 2011). It has an extensive fossil record that extends back to the Triassic (Evenhuis, 1994). Although the systematic position of the group is a contentious issue, some hypotheses point to the Tipulomorpha as the sister group to the rest of the Diptera [for details about the different hypotheses on the systematic position of the Tipulomorpha, see Ribeiro (2008)] or at least branching near the base of the Diptera tree (Wiegmann *et al.*, 2011).

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Crane fly species display a high level of endemism (De Jong *et al.*, 2008): thus Oosterbroek (1994) estimated that, in the Mediterranean region, species of the family Tipulidae display higher levels of endemism than other insect groups (lacewings and butterflies), and that, on average, they have more limited distributions than observed in these other groups of insects and in vertebrates.

Inhabiting a diverse range of environments (Alexander, 1919, 1920; Alexander & Byers, 1981) and present for at least the last 208 million years (Krzeminski, 1992; Krzeminski & Evenhuis, 2000), crane flies can potentially inform about the biogeographical history of terrestrial ecosystems. If explored in detail, crane fly distribution patterns provide valuable data for biogeography.

The southern hemisphere has been a preferred region for historical biogeographical studies (Sanmartín *et al.*, 2001). Paradoxically, most biogeographical studies on crane flies focus on the northern hemisphere (Oosterbroek, 1980; Tangelder, 1988; Oosterbroek & Arntzen, 1992; De Jong, 1998; Gelhaus, 2005).

A major question for the study of south hemisphere biogeography refers to the feasibility of alternative explanations for the biotic links between southern South America, New Zealand, Australia and the biogeographically related areas of New Guinea and New Caledonia. In one hand, there is the tendency to consider southern hemisphere disjunctions in general simply as Gondwanan. For instance, De Jong *et al.* (2008) refer to distributional patterns of crane flies in the southern hemisphere as Gondwanan, although acknowledging that 'A closer look at the taxa involved reveals more intricate patterns: four genus-group taxa are present in New Zealand, Australia, and the Neotropical region, four taxa are exclusively found in New Zealand and the Neotropical region, and four taxa are exclusively shared by Australia and the Neotropical region (De Jong *et al.*, 2008: 465)'.

As stated by McCarthy *et al.* (2007): 'A number of recent papers that have also focused on southern trans-Pacific disjunctions have only strengthened the trans-Pacific bond. This should seem remarkable given that in conventional reconstructions Australia and South America are on opposite sides of Gondwana with South Africa in between them.' So the question raised is whether current accepted palaeogeographical reconstruction of Gondwana is a sufficient model for explaining all southern hemisphere disjunctions (whether by vicariance or dispersal). Although many well documented trans-Atlantic disjunctions undoubtedly fit into the model [for examples within crane flies, see De Jong *et al.* (2008)], many cases of trans-Pacific disjunctions suggest that Gondwana, as an explanatory model, may be incomplete. Trans-Pacific disjunctions have stimulated the proposal of alternative reconstructions of Gondwana (e.g. McCarthy *et al.*, 2007) or even more radical views such as the hypothesis of a completely enclosed Pacific basin in the Mesozoic (McCarthy, 2003, 2005, 2007).

Hypotheses of biogeographical homology are the basis of historical biogeography, and progress in biogeography can be achieved by two related, although independent, steps (Morrone, 2001).The first would be the formulation of primary hypotheses

of biogeographical homology, which 'refers to a conjecture on a common biogeographic history, which means that different plant and animal taxa are spatiotemporally integrated in a biota' (Morrone, 2001: 298). A panbiogeographical analysis, in which biogeographical patterns (generalised tracks) are proposed from the comparisons of repetitions of individual distributions (individual tracks) would deal, according to Morrone (2001), precisely with the formulation of primary hypotheses of biogeographical homology. The second step of the biogeographical inquiry would be the testing of the proposed hypotheses by cladistics biogeographical methods.

This research attempts to answer the following question: To what extent do the distribution patterns of crane flies in the southern hemisphere provide evidence of biogeographical homology (i.e. shared history) in the South Pacific? The question is relevant because area homologies – depictions of biotic relationships between areas – allow biotic areas to be compared with hypothesised geological history over time and space (Parenti & Ebach, 2009).

Until now, systematic work on crane flies focused mostly on the description of its enormous diversity and our current knowledge on the evolutionary biology of the group is rudimentary. Because sound hypotheses of relationships between taxa form the basis of good biogeographical interpretations, exploring the full potential of crane flies for biogeography will require many years of research. However, despite a lack of comprehensive phylogenetic studies, some phylogenetic hypotheses (Vane-Wright, 1967; De Jong, 1989; Ribeiro, 2008, 2009) provide a background for interpreting and discussing the distribution patterns in light of a partial established systematic framework. Nevertheless, many taxa endemic to this part of the world remain to be treated in a phylogenetic context. In a general discussion, these taxa at least offer information on diversity and endemism patterns, and provide some measure of the great potential of future systematic and biogeographical research.

Contrasting views: crane flies and southern hemisphere biogeography

The numerous southern disjunctions within Tipulomorpha have drawn attention and the opinions of two outstanding entomologists, Charles Paul Alexander and Willi Hennig, are of special interest.

Charles Paul Alexander – the author of over 11 000 crane fly species and more than 200 genera and subgenera (Oosterbroek, 2009) – has described most of the taxa dealt with in this paper. In his taxonomic reports, Alexander often discussed his views on the taxonomic affinities of the taxa under consideration. In some instances, his comments on relationships have been supported by modern systematic studies (De Jong, 1989; Ribeiro, 2008, 2009). Clearly, several examples of southern trans-Pacific disjunctions treated by subsequent workers (including those given here) were known, and commented upon, by Alexander. Notably, already in the late 1940s, Alexander (1948a) seemed to be convinced by Wegener's hypothesis of continental drift, on the basis of the

Neotropical–Afrotropical distribution of the crane fly genus *Lecteria*. As discussed below, Alexander considered the distribution patterns of crane flies in the southern hemisphere as strong evidence of direct biogeographical links between different continents. In other words, the disjunctions had to be caused by the fragmentation of an ancestral biota. The exact means by which this could have happened were, of course, poorly known in his time.

In his monograph on the crane flies of Argentina and South Chile, Alexander (1929a) made the following comments on the affinities of the southern South American fauna:

'The first impression gained from a survey of the Tipulidae [Tipulidae sensu lato, = Tipulomorpha of the classification system adopted herein] of Patagonia and southern Chile is the marked resemblance to the Australasian fauna, and upon critical analysis it is found that a considerable proportion of the genera, subgenera and certain groups of species are common to the two regions. The fact has long been known and appreciated that identical genera or other closely allied groups of plants and animals are to be found in southern South America and again in the Australasian Region, more especially in New Zealand, and the colder south-eastern parts of Australia, as Tasmania and the mountains of Victoria and New South Wales. In a lesser number of cases, the distribution of the included forms is carried much further to the north, into southern Brazil on the one hand and to northern Australia, New Guinea or New Caledonia on the other' (Alexander, 1929a: 5).

Hennig (1960), in a detailed survey of biogeographical affinities in the New Zealand Diptera (Hennig, 1966 as translated into English), criticised the taxonomic treatment of the crane flies, for which no phylogenetic studies were available. Thus, he concluded that the distributions could not be regarded as strong evidence of direct links between New Zealand, South America and Australia. He interpreted most disjunctions from a dispersalist point of view (considering the northern hemisphere as a major centre of origin), and seemed focused on dismissing any evidence of direct southern connections in Diptera as unsupported. Vane-Wright (1967) discussed the relationships and biogeography of the southern disjunct Tipulidae genera *Ischnotoma* and *Zelandotipula*, and adopted the dispersalist approach of Hennig (1960, 1966). In contrast, Brundin (1966), studying the Chironomidae (Diptera), strongly supported southern connections and vicariance. De Jong (1989) was one of the first authors to study the systematics and biogeography of southern hemisphere crane flies from a cladistic point of view. He discussed the phylogenetic relationships between the South American Tipulidae taxa *Elnoretta*, *Euvaldiviana* and *Valdiviana*, and concluded they belonged to a clade with two other genera endemic to Australia. De Jong (1989) suggested that the sequence of breakup of Gondwana would be the best explanation for this disjunction. In a study mostly devoted to understanding the early evolution of crane flies, Ribeiro (2008) provided additional examples of clades with restricted distributions in south temperate areas. The phylogeny and biogeography of the trans-Pacific subfamily Stibadocerinae (family Cylindrotomidae) was analysed in Ribeiro (2009). All these recent cladistic studies (De Jong, 1989; Ribeiro, 2008, 2009) have supported at least some of Alexander's views on the affinities of taxa.

Materials and methods

Qualitative analysis

The assembling of the data for the analysis of distributional patterns involved several steps of compilation and cross-checking. Most data were retrieved from the *Catalogue of the Crane Flies of the World* (Oosterbroek, 2011; CCW, which is an authoritative, regularly updated database that covers all of the over 17 000 genus-group and species-group taxa of the families Pediciidae, Limoniidae, Cylindrotomidae and Tipulidae. The level of geographical detail provided by CCW varies: for some areas, species distributions are given by country only, as is the case for Europe, Africa and South America, but for others (for instance, China, Australia, U.S.A., India, Malaysia, Russia, Japan, among others), the details extend to states and provinces. For this survey, the level of geographical detail given by CCW generally is satisfactory. The only exception concerns South America. For this large continent, species distribution given by country only was insufficient and so the details for distributions of South American species were complemented by information derived from the taxonomic literature. The original descriptions of many taxa were used as a complementary source of information. The catalogue of Alexander & Alexander (1970) was also useful as a source of information on localities.

The first step of the compilation was the listing of all genera, subgenera and species occurring in selected countries from both the southern and northern hemispheres, namely Argentina, Australia, Chile, India, Indonesia, Madagascar, Malaysia, New Caledonia, New Guinea, New Zealand, Paraguay, Philippines, Singapore and South Africa. The selection of these first areas, although arbitrary, was important for the second step of the compilation, which consisted of cross-checking the entire (global) distribution of all the genera and subgenera surveyed in the first step. Because most of the taxa occurring in the first selected countries are shared by different combinations of many other areas, the second step of the compilation created a very large database on the distribution of over 70 genera and subgenera occurring not only in the southern hemisphere. The process did not exhaust the distribution patterns of all taxa, but nevertheless the compilation undoubtedly generated enough data for addressing the question pointed out in the Introduction.

The third step was the detailed study of the distributional data of the taxa. The distribution information was synthesised in the form of maps, to allow direct visual comparison and distinction of patterns. Interpretation of the maps followed the reasoning of panbiogeography (Craw *et al.*, 1999). This included the recognition as biogeographical patterns (generalised tracks) from the observed repetitions of particular distributions (individual tracks), where repeating distribution

patterns are interpreted as conjectures on a common history (biogeographical homology) between the areas.

Numerical analysis

Parsimony analysis of endemicity is considered a quantitative technique of the panbiogeographical approach (Morrone, 2001). This kind of analysis was performed in order to test whether the patterns involving South Pacific disjunctions that resulted from the qualitative survey would emerge from a quantitative analysis. A presence/absence data matrix was created including all 205 recognised genera of crane flies and 183 countries as provided in CCW. The construction of this large data matrix was possible by exporting from CCW (in Excel format) lists of all the genera occurring in every country. The data matrix was translated from Excel format into Nexus (.nex) format using the software PAST, version 2.07 (Hammer *et al.*, 2001), and then exported into HENNIG (.ss) format using the software NEXUS DATA EDITOR (Page, 2001). The matrix in HENNIG format was analysed numerically with a parsimony algorithm in TNT (Goloboff *et al.*, 2003) using implied weighting (k value = 3) with the option 'New Technology Search' (up to 10 000 trees in memory; 1000 replications). Versions of the data matrix to open in PAST, NEXUS DATA EDITOR (.nex) and TNT (.ss) format are available as Table S1.

Results and discussion

Analysis of the distribution, diversity and endemism patterns of crane flies by both the qualitative and numerical analyses revealed a neat and clear pattern, linking southern South America and Australasia, providing evidence of biogeographical homology (i.e. shared history) in the South Pacific. The results not only corroborate the hypothesis of strong historical links between these areas, but also suggest vicariance as a major cause for these austral disjunctions.

The parsimony analysis of endemicity of the data matrix yielded 1136 most-parsimonious reconstructions. The strict consensus shows that, in all these topologies, a group linking southern South America with Australasia is formed in the following order: ((New Zealand + (Argentina + Chile))) + ((New Caledonia + (Australia + (Indonesia + Papua New Guinea)))). This result should not be considered as any hypothesis of hierarchical relationships between these areas. This pattern is interpreted here solely as a primary hypothesis of biogeographical homology between these areas, i.e. 'a conjecture on a common biogeographic history' (Morrone, 2001: 298) meaning that different crane fly taxa are spatiotemporally integrated in a trans-Pacific biota.

The distributional information of the groups depicting the southern South America–Australasia patterns is summarised in Figs 1–16. In these maps, the shaded areas link, within each continent, the areas of occurrence of the taxa. This graphic device was used here mostly as a way of highlighting the distributions for comparison and identification of patterns.

They do not imply that the geographical distribution of the taxa necessarily spans the complete area shaded.

Thirty genera and subgenera, including about 700 species, occur exclusively within the limits of what has been called the South Pacific Track (SP-Track) by Crisp *et al.* (1999). Heads (2006) referred to this pattern simply as the South Pacific disjunction. The same track has been named as the Austral–Antarctic Track by Moreira-Munoz (2010). Twenty of these genera/subgenera belong to clades recovered by the phylogenetic studies of Vane-Wright (1967), De Jong (1989) and Ribeiro (2008). Some of these clades are partially congruent with standard biogeographical patterns recovered for the southern hemisphere by previous studies (e.g. Sanmartín & Ronquist, 2004). For the remaining taxa, the lack of phylogenetic knowledge prevents deeper biogeographical interpretations, but nevertheless their diversity and endemism patterns corroborate what is observed for the other groups and for crane flies in general.

Remarkably, for these genera and subgenera occurring exclusively within the SP-Track, all species are endemic to just one continental area. Few examples of truly widespread crane fly species (occurring also in Australia, New Zealand, New Guinea and New Caledonia) are known, for example, in the genera *Conosia*, *Symplecta*, *Discobola*, *Trentepohlia*, *Atypophthalmus* and *Dicranomyia* (Oosterbroek, 2011). The known examples of widespread crane fly species do not exceed one or two in each of the mentioned genera (De Jong *et al.*, 2008) and are exceptions. If trans-oceanic dispersal were common for the crane flies, one should expect that this process would have happened constantly over time. At least some species of the very many genera/subgenera treated here would be expected to have dispersed recently and would be shared between different austral continents. In fact, the high level of species endemism is compatible with allopatric differentiation and supports vicariance as the main process behind crane fly disjunctions in this part of the world.

Crisp *et al.* (1999) suggested that the SP-Track is composed of two elements. The southern and best-known element links southern South America, New Zealand and Australia. There is a vast amount of palaeobotanical evidence supporting past connections between these areas. The second element, less studied, involves distributions in New Caledonia, New Guinea, West Malesia (Java, Sumatra, Borneo and Sulawesi) and Fiji. The geological histories of New Caledonia and New Guinea are complex, including accretion of terrenes of different origins (Heads, 2006, 2010). Whatever the geological history, crane fly data include New Caledonia and New Guinea in the SP-Track.

The biogeography of New Zealand has also been an issue of strong recent debate [for a recent revision of this debate, see Giribet & Boyer (2010)]. Our results provide support for multiple trans-Pacific and trans-Tasman Sea disjunctions that are explained most simply by continental drift. Nevertheless, the distributions dealt with here can hardly be considered simply as Gondwanan, because neither Africa nor India is involved. Because all the disjunctions analysed are centred at the Pacific Ocean, regarding them as trans-Pacific is preferable to treating them as Gondwanan.
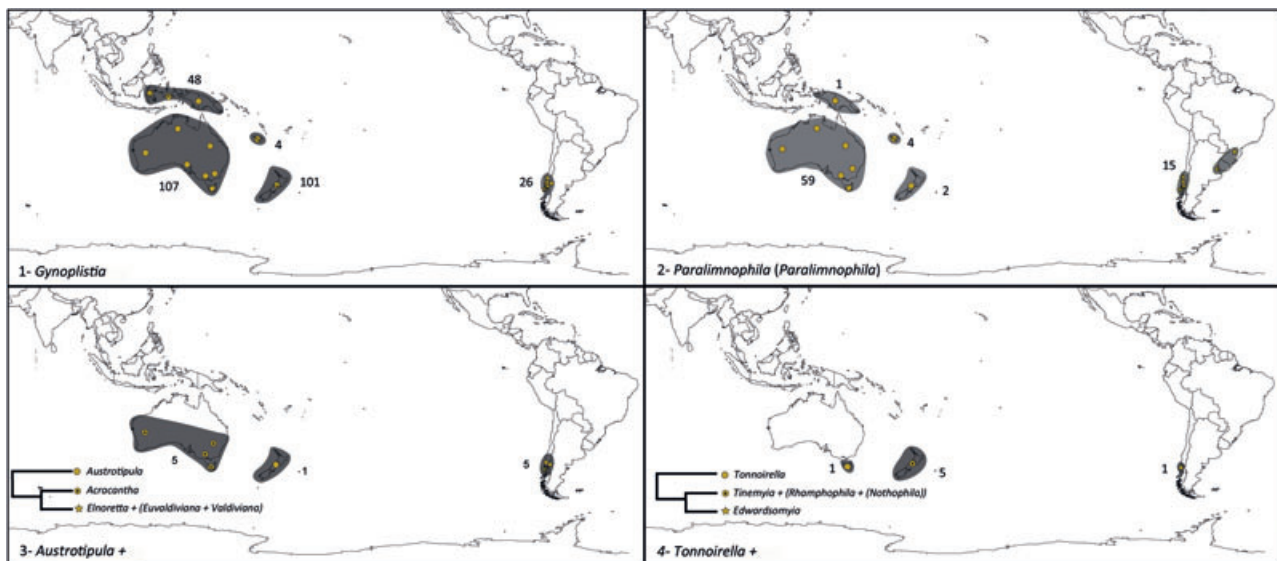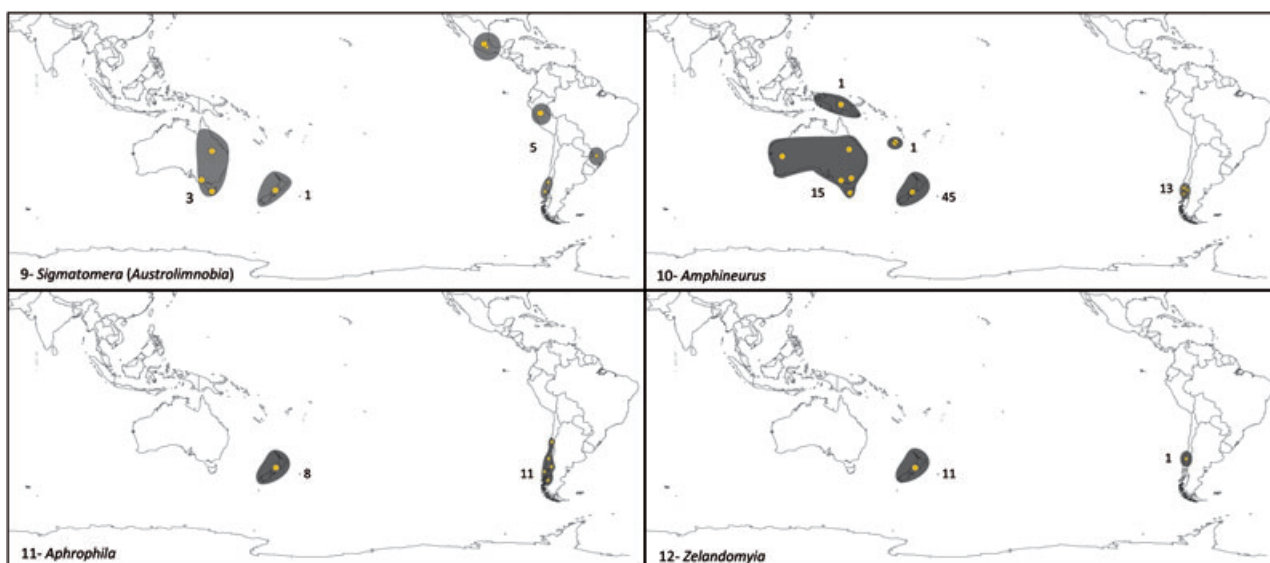
Figs 1–4. Trans-Pacific distributions of Tipulomorpha. 1, *Gynoplistia* (sensu lato). 2, *Paralimnophila* (*Paralimnophila*). 3, *Austrotipula* and related genera. 4, *Tonnoirella* and related genera. Asterisks indicate more precise information on species distributions in South America as complemented by taxonomic literature. Circles and other figures indicate distributional data as given by *Catalogue of the Crane Flies of the World* (Oosterbroek, 2011; countries and provinces). Numbers indicate the number of described species in each area.
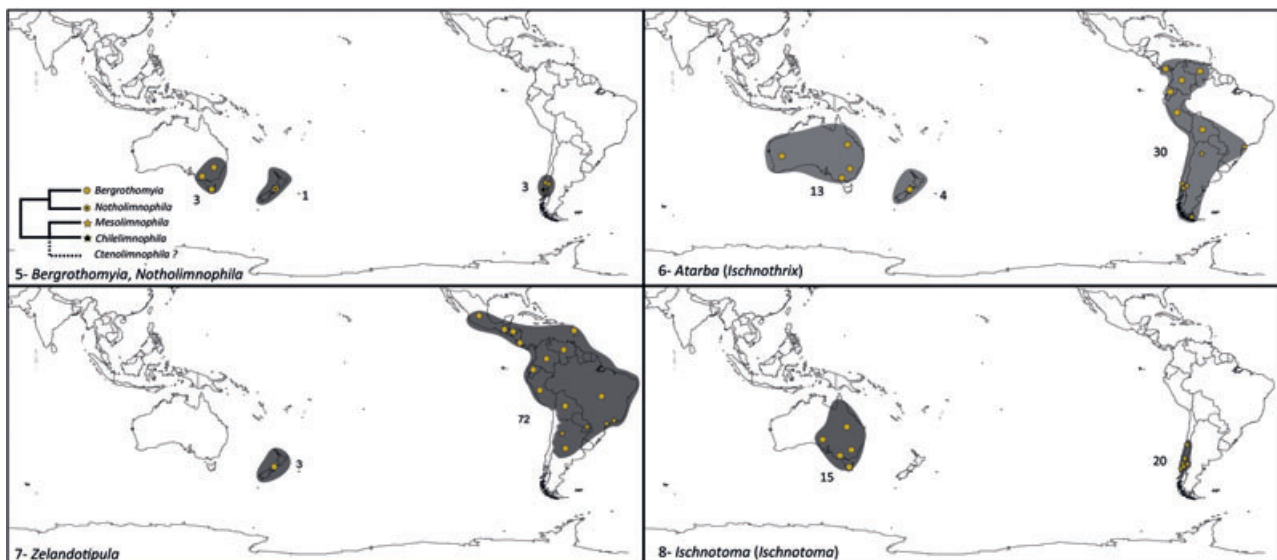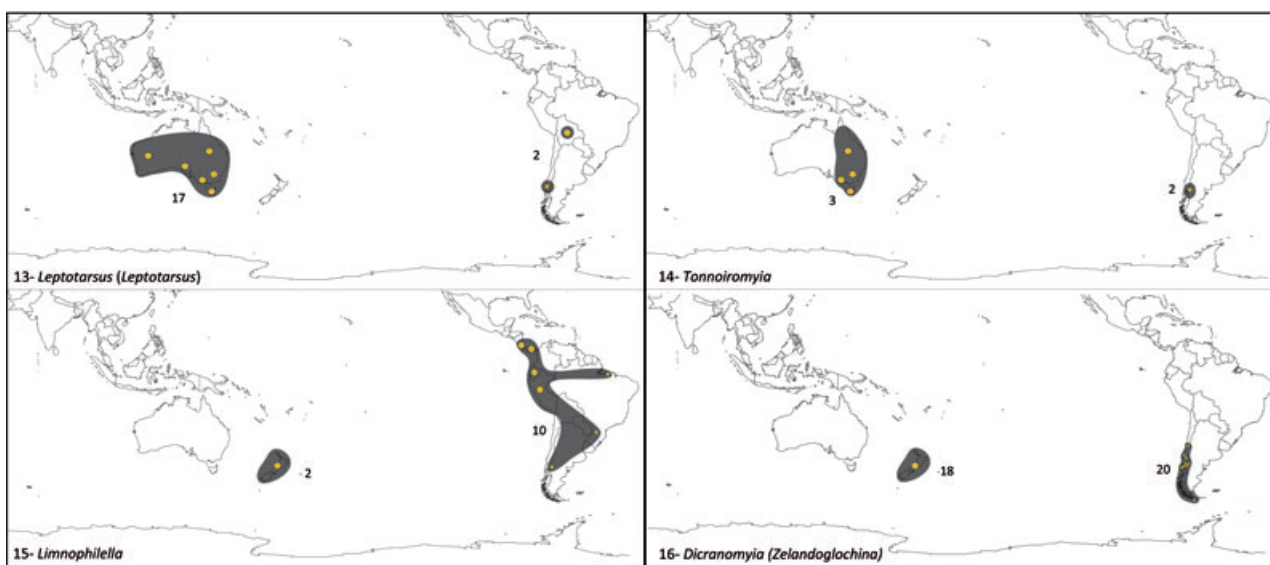

Figs 5–8. Trans-Pacific distributions of Tipulomorpha. 5, *Bergrothomyia* and related genera. 6, *Atarba* (*Ischnothrix*). 7, *Zelandotipula*. 8, *Ischnotoma* (*Ischnotoma*). Asterisks indicate more precise information on species distributions in South America as complemented by taxonomic literature. Circles and other figures indicate distributional data as given by *Catalogue of the Crane Flies of the World* (Oosterbroek, 2011; countries and provinces). Numbers indicate the number of described species in each area.

Whatever the case, the distribution patterns studied here argue against a recent arrival of the New Zealand crane fly fauna. For many of the trans-Pacific groups mapped here, New Zealand is not just involved, but is the main centre of diversity, which also suggests a long history of in situ evolution. In the family Chironomidae, another group of Diptera common in austral regions, Cranston *et al.* (2010) concluded that some New Zealand taxa are not post-Oligocene colonists, and reaffirmed the conclusion of Brundin (1966), that the affinities of the New Zealand Chironomidae were closer to South American taxa than to Australian. Recent studies of the phylogeny and biogeography of New Zealand's invertebrates (reviewed by Giribet & Boyer, 2010) convincingly counter the 'complete drowning' scenario.

Figs 9–12. Trans-Pacific distributions of Tipulomorpha. 9, *Sigmatomera* (*Austrolimnobia*). 10, *Amphineurus*. 11, *Aphrophila*. 12, *Zelandomyia*. Asterisks indicate more precise information on species distributions in South America as complemented by taxonomic literature. Circles and other figures indicate distributional data as given by *Catalogue of the Crane Flies of the World* (Oosterbroek, 2011; countries and provinces). Numbers indicate the number of described species in each area.

Figs 13–16. Trans-Pacific distributions of Tipulomorpha. 13, *Leptotarsus* (*Leptotarsus*). 14, *Tonnoiromyia*. 15, *Limnophilella*. 16, *Dicranomyia* (*Zelandoglochina*). Asterisks indicate more precise information on species distributions in South America as complemented by taxonomic literature. Circles and other figures indicate distributional data as given by *Catalogue of the Crane Flies of the World* (Oosterbroek, 2011; countries and provinces). Numbers indicate the number of described species in each area.

Although some South Pacific taxa have distributions that span the entire track, others are present in parts of the track only, forming the following nested set of distributions (see also Table 1):

1. Complete SP-Track (South America–New Zealand–Australia–New Caledonia–New Guinea) (three genera/subgenera) (Figs 1, 2, 10).

2. South America–New Zealand–Australia (16 genera/subgenera) (Figs 3–6, 9).

3. South America–New Zealand (five genera/subgenera) (Figs 7, 11, 12, 15, 16).

4. South America–Australia (three genera/subgenera) (Figs 8, 13, 14).

Table 1. Nested set of distributions of taxa and clades within the South Pacific Track.

Complete track (South America–New Zealand–Australia–New Caledonia–New Guinea)	South America–New Zealand–Australia	South America–New Zealand	South America–Australia
Gynoplistia (sensu lato)	((*Austrotipula* + (*Acracantha* + (*Elnoretta* + (*Euvaldiviana* + *Valdiviana*))))	*Zelandotipula*	*Ischnotoma* (*Ischnotoma*)
Paralimnophila (*Paralimnophila*)	((*Tonnoirella* + (*Edwardsomyia* + (*Tinemyia* + (*Rhamphophila* + (*Nothophila*))))))	*Aphrophila*	*Leptotarsus* (*Leptotarsus*)
Amphineurus	(((*Notholimnophila* + *Bergrothomyia*) + (*Mesolimnophila* + (*Chilelimnophila* + *Campbellomyia*))))	*Zelandomyia*	*Tonnoiromyia*
	Atarba (*Ischnothrix*)	*Limnophilella*	
	Signatomera (*Austrolimnobia*)	*Dicranomyia* (*Zelandoglochina*)	

These more restricted subpatterns could be explained by extinctions in areas where taxa were present previously. Alternatively, in some cases the pattern may indicate historical absences and the existence of a heterogeneous set of ancestral distributional ranges.

Distributions of some genera extend in South America beyond the temperate zone into tropical areas. This pattern follows two main tracks, also seen in different groups of plants (Moreira-Munoz, 2010). One track has been referred to as the Central Andean Track, linking southern South America to the northern lands via the Andes. Another, and very interesting pattern, encompasses disjunctions of taxa found in Chile, northern Argentina, Uruguay, Paraguay and southeastern Brazil (Moreira-Munoz, 2010). The distribution of *Paralimnophila* (*Paralimnophila*) in South America is a clear example of a south central Chile–southeastern Brazil disjunction.

Synopsis of the fauna

A summary of the fauna is given below. The taxa for which some phylogenetic knowledge is available are discussed with more detail. The complete authored names of the genus-group taxa discussed in this section or mentioned in previous parts of the text are provided in the Appendix.

Gynoplistia [Family Limoniidae] (Fig. 1)
Gynoplistia is diverse, with over 340 described species in four subgenera: *G.* (*Cerozodia*), *G.* (*Dirhipis*), *G.* (*Gynoplistia*) and *G.* (*Xenolimnophila*). The distribution of the subgenus *Gynoplistia* (the largest subgenus, with 319 described species) replicates the distribution of the whole genus, the typical SP-Track. There is some overlap in the distribution of the subgenera, a situation that recalls that of *Nothofagus* (Heads, 2006). *Gynoplistia* (*Gynoplistia*) occurs in southern South America, New Zealand, New Caledonia, New Guinea and Australia. *Gynoplistia* (*Cerozodia*) occurs in Australia and New Zealand. *Gynoplistia* (*Dirphipis*) occurs in southern South America (Chile and Argentina) and *G.* (*Xenolimnophila*) is in Australia only.

In the most recent taxonomic treatment of *Gynoplistia*, Theischinger (1993, 1994a) revised the Australian species. One fossil species, *G. mitchelli* Jarzembowski, was described for the Lower Cretaceous of England (Evenhuis, 1994).

Alexander (1948b) regarded the distribution of the genus *Gynoplistia* as highly significant for biogeography:

'In my opinion, this single genus provides an almost unbreakable link in the long chain of evidence supporting a belief in a former Antarctic land connection' (Alexander, 1948b: 525).

Hennig (1960, 1966) was sceptical of Alexander's views and wrote:

'There is no reason to suppose that there exists a sister-group relationship between Chilean Dirhipis and the Australian subgenera' (Hennig, 1966: 21).

The genus was included in the phylogenetic study of the Tipulomorpha by Ribeiro (2008) and the monophyly of the

entire genus was not recovered. However, at least one clade including most of the sampled terminal taxa of the subgenera *Cerozodia*, *Gynoplistia* and *Dirhipis* is supported. Therefore, available evidence supports the monophyly of the bulk of the group. Also, the monophyly of the subgenera *G*. (*Cerozodia*) and *G*. (*Dirhipis*) is also supported (Ribeiro, 2008).

Interestingly, in the study of Ribeiro (2008), this clade appears as the sister group of one of the sampled species of the genus *Paralimnophila*. Regarding this relationship, Hennig (1966: 21) commented:

'If *Gynoplistia* and *Paralimnophila* were really monophyletic groups and additionally sister-groups, then *Gynoplistia* sensu lato would really show a distribution pattern which could be reduced to the scheme illustrated in Fig. 3 (a direct trans-Antarctic link between South America, Australia and New Zealand), and the genus would indeed represent a weight argument in support of the hypothesis of a former Antarctic land connection, as expressed by Alexander.[...] As long as such a prove is not available, it can always be suspected that the apparent AS-relationship found in two very closely related groups (sister-groups), which seems to exist in the Genus *Gynoplistia*, is really an artifact due to the method (not strictly phylogenetic) applied'.

Paralimnophila (Paralimnophila) [Family Limoniidae] (Fig. 2)

Paralimnophila includes about 100 described species, most of which belong to the nominotypical subgenus. The genus was recently diagnosed by Theischinger (1996a). The subgenus *P*. (*Papuaphila*) comprises 14 species endemic to New Guinea (13 species) and Maluku (one species). *Paralimnophila* (*Paralimnophila*) includes the rest of the diversity of the genus, also distributed throughout the SP-Track, and with a few species also occurring in northeastern Argentina and southeastern Brazil. Only the Australian species (all in the subgenus *Paralimnophila*) have been recently revised (Theischinger, 1996a). A detailed revision and phylogenetic study of this genus would probably be very rewarding. The geographical distribution of the genus *Paralimnophila*, centred at the Pacific Basin, and absent from typical Gondwanan areas such as South Africa and India is remarkable.

An unnamed clade in Tipulidae: (*Austrotipula* + (*Acracantha* + (*Elnoretta* + (*Euvaldiviana* + *Valdiviana*)))) (Fig. 3)

Alexander (1929a, 1969) considered *Valdiviana* and *Elnoretta* closely related to *Austrotipula* and *Acracantha*. The clade ((*Austrotipula* + (*Acracantha* + (*Elnoretta* + (*Euvaldiviana* + *Valdiviana*))))) was discovered by De Jong (1989). *Austrotipula* has one species in New Zealand; *Acracantha* includes three species in Australia (New South Wales, Victoria, Tasmania and Western Australia); the entire ((*Elnoretta* + (*Euvaldiviana* + *Valdiviana*))) clade is restricted to southern South America (the whole clade includes five species in Chile and Argentina). The monophyly of each of these genera and of the different nodes of the entire clade is discussed by De Jong (1989). These genera are unknown in the fossil record.

This clade is consistent with one of the major hierarchical biogeographical patterns reviewed by Sanmartín & Ronquist

(2004): the Southern Gondwana Pattern: Africa + ((New Zealand + (Southern South America + Australia))). As stated by Sanmartín & Ronquist (2004), this pattern is the most common one found in southern hemisphere biogeographical studies [including the classic study of Brundin (1966)]. It is consistent with the assumed sequence of fragmentation of Gondwana and can thus be explained as the result of vicariance.

To agree completely with the Southern Gondwana Pattern, this crane fly clade would need an element in Africa that it lacks. Concerning the absence of other connections, the concluding remarks of De Jong (1989) are interesting:

'The monophyletic group containing *Austrotipula*, *Acracantha*, *Elnoretta*, *Euvaldiviana* and *Valdiviana* probably represents one of the oldest phylogenetic lines of Tipulidae. The absence of an Afrotropical member in this unit suggests that it originated during the early or middle Cretaceous after the separation of Africa from Antarctica and prior to the separation of New Zealand from that continent (115–80 million of years). The small number of species described in the genera may be indicative of their relict character. [...]. The sister group of the monophyletic group dealt with in this paper is most likely to be found among the ancient Tipulidae inhabiting the southern hemisphere, but, as stated above, the inadequate definition of many of these taxa obstructs the establishment of this connection. There seems to be no close relationship between the austral group containing *Acracantha*, *Austrotipula*, *Elnoretta*, *Euvaldiviana* and *Valdiviana* and Tipulidae from the boreal zone'.

De Jong's (1989) interpretation of the biogeography of this clade is no doubt in agreement with a widely accepted palaeogeographical scenario. However, the possibility exists that this group may in fact be 'relict', not of Gondwana, but of an ancestral trans-Pacific biota, as suggested by the repeating distribution patterns of the other crane fly groups discussed here. In this case, the absence of any obvious connection with other Gondwanan areas is not surprising.

An unnamed clade in Limoniidae: ((*Tonnoirella* + (*Edwardsomyia* + (*Tinemyia* + (*Rhamphophila* + (*Nothophila*)))))) (Fig. 4)

Alexander (1928, 1929a, 1948a) considered *Tonnoirella*, *Tinemyia*, *Rhamphophila*, and *Edwardsomyia* to be closely related. *Tonnoirella* includes one species (with two subspecies) from Tasmania; *Edwardsomyia*, monotypic, occurs only in south Chile; *Tinemyia* also has one species, restricted to New Zealand; *Rhamphophila* and *Nothophila* have two species each, restricted to New Zealand. There are no known fossil representatives belonging to any of these genera. A clade including these genera plus *Nothophila* was recovered by Ribeiro (2008), who also discussed the synapomorphic characters supporting its internal relationships. The monophyly of each of these genera seem beyond doubt. Most of them are monotypic and very distinctive groups. The two include species of *Nothophila* included in the phylogenetic study of Ribeiro (2008) and the monophyly of the genus is supported. A single species of *Rhamphophila* (*R. sinistra*) was included in

the analysis of Ribeiro (2008), but its autapomorphic characters hold true for the other species of the genus (*R. lyrifera*).

The relationships depicted by this clade are inconsistent with the South Gondwana Pattern of Sanmartín & Ronquist (2004), but agree with the pattern named by these authors as the Inverted Southern Pattern: Africa + (Australia + (southern South America + New Zealand)). Again, complete agreement is prevented by the lack of any robust or obvious connection with Africa. The sister group of this clade in the preferred tree in Ribeiro (2008) is *Austrolimnophila*, a very large genus present in part of the Afrotropical region, but also in many other places.

According to Sanmartín & Ronquist (2004), the Inverted Southern Pattern is incongruent with the putative sequence of breakup of Gondwana and is normally explained as dispersal, or by some alternative vicariance sequence. The possibility that the speciation events responsible for the branching of this clade occurred before the breakup of Gondwana – as hypothesised by Heads (2006) for the plant genus *Nothofagus* – should also be taken into consideration, especially assuming the possibility of a Late Paleozoic or early Mesozoic origins of some extant crane fly lineages (Wiegmann *et al.*, 2011).

An unnamed clade in Limoniidae: (((*Notholimnophila* + *Bergrothomyia*) + (*Mesolimnophila* + (*Chilelimnophila* + *Campbellomyia*)))) (Fig. 5)

This clade was recovered by Ribeiro (2008). *Notholimnophila* is monotypic and endemic to New Zealand; *Bergrothomyia* includes three species in Australia (Victoria, New South Wales) and Tasmania; *Mesolimnophila* has two species in south Chile; *Chilelimnophila* is monotypic and endemic to south Chile. Its status as a distinct genus was recently reaffirmed by Ribeiro (2007). *Campbellomyia* is a subgenus of *Ctenolimnophila* with seven species in New Zealand, two in southeast Brazil near the Atlantic margin, one species in Bolivia and Ecuador, and one in Madagascar. There are no fossil taxa described for any of these groups.

The clade has a fairly intricate distribution that does not fit in any of the major hierarchical patterns of Sanmartín & Ronquist (2004). This may have different explanations. Not all parts of this clade are strongly corroborated by morphological evidence. Critically, the *Chilelimnophila* + *Campbellomyia* component lacks unambiguous character support (Ribeiro, 2008). The nonmonophyly of *Ctenolimnophila* and its included subgenera may not be completely discarded. In short, the affinities of the genera included in this clade need further study. The apparent 'gathering' of these mostly southern temperate genera into a single clade, however, is noteworthy, and probably reveals some weak phylogenetic and biogeographical signal in need of further clarification. Of special relevance is the putative sister-group relationship between *Bergrothomyia* and *Notholimnophila*, supporting the reality of a trans-Tasman track. Further examples of Dipteran taxa displaying strictly Australian/New Zealand sister-group relationships are provided by Cranston (2005).

Atarba (*Ischnothrix*) [Family Limoniidae] (Fig. 6)

Atarba is a large genus with three subgenera, *A.* (*Atarba*) [81 spp.], *A.* (*Atarbodes*) [29 spp.] and *A.* (*Ischnothrix*) [48 spp.]. The Australian species were revised by Theischinger (1994b, 1996b). The affinities among and within its subgenera are unknown.

The distribution of *A.* (*Ischnothrix*) has already been noted by Alexander (1929a), but Hennig (1960, 1966) felt suspicious about its monophyly and of its distribution as evidence for trans-Antarctic connections.

Atarba was represented in the recent study of Ribeiro (2008) by one terminal taxon and the systematic position of the genus could not be well established within the Limnophilinae. Ribeiro (2008) suggested the group may be related more closely to taxa within the Limoniinae (Oosterbroek & Theowald, 1991) or Chioneinae. However, Petersen *et al.* (2010) corroborated the systematic position of the group as proposed by Ribeiro (2008) in a clade together with *Elephantomyia* and *Helius*.

One *Atarba* species not assigned to a subgenus is known from the Eocene/Oligocene of England (Evenhuis, 1994).

Zelandotipula and *Ischnotoma* (*Ischnotoma*) [Family Tipulidae] (Figs 7, 8)

Ischnotoma (*Ischnotoma*) includes 20 species in southern South America and 15 species in Australia. *Zelandotipula* is mostly a Neotropical group (over 70 species in tropical and subtropical South America) with three known species in New Zealand. Alexander (1929a) suggested a close relationship between *Ischnotoma*, *Zelandotipula* and *Holorusia*. Hennig (1960, 1966) questioned these possible relationships. Vane-Wright (1967) revised these taxa and their relationships and concluded that *Zelandotipula* is probably not closely related to *Holorusia* or *Ischnotoma*, but that *Holorusia* and *Ischnotoma* may be sister groups. The putative apomorphic characters supporting the monopyly of these genera and their relationships are discussed by Vane-Wright (1967).

Regarding the disjunct distribution of *Ischnotoma* in South America and Australia, Vane-Wright (1967: 527–526) declared:

'The present centre of distribution of *Holorusia* is north India and south-east Asia [...], and it would appear that the present species have radiated from this region to the west into the Ethiopian region, and to the east to northern Australia, Fiji and Japan, and perhaps via the Bering Sea to the western coast of North America [...]. If *Ischnotoma* is truly closely related to *Holorusia*, the former genus may have become confined to the extremities of South America and Australia by displacement as a result of competition, reaching the areas originally from the North, as Hennig (1960) suggests as a possibility. This idea is supported by the genus being represented by apparently quite distinct subgenera in the two regions concerned, although the total absence of both *Ischnotoma* and *Holorusia* from large areas, especially tropical America, does not strength this view. Unfortunately I have not seen *Ischnotoma penai* or *I. problematica*, both described by Alexander, from Chile. These species may prove to be vital intermediates between *Ischnotoma* sensu stricto and *Ischnotoma* (subgenus *Icriomastax*), making it possible to suggest that *Ischnotoma* reached S. America via an Antarctic land bridge or connection'.

Regarding *Zelandotipula*, Vane-Wright (1967: 529) concluded:

'*Zelandotipula*, occurring to the northern half of South America, and in New Zealand, might have reached these areas from the north also. However, no traces of the genus exist elsewhere [. . .]. The present ocean currents from the western equatorial region of South America travel in an appropriate direction to carry eggs or larvae to New Zealand [. . .]. This would provide a convenient explanation of the present distribution, but is obviously difficult to prove [. . .]. However, distribution by the "direct"(Antarctic) or "indirect" (Northern) routes seems unlikely, as does introduction of the genus by man into New Zealand (probably providing too little time for the speciation already achieved)'.

Sigmatomera (*Austrolimnobia*) [Family Limoniidae] (Fig. 9)

Sigmatomera is a small genus with 23 described species in four subgenera: *S*. (*Austrolimnobia*) [9 spp.], *S*. (*Eufurina*) [1 sp.] and *S*. (*Sigmatomera*) [13 spp.]. The group occurs mainly in tropical areas of South America, with only the subgenus *S*. (*Austrolimnobia*) known from the southernmost parts of the globe, in Chile (two species), New Zealand (one species) and Australia (three species).

The genus is unknown as fossils. The phylogeny of the included species has never been investigated, but the genus is easily recognisable morphologically (Alexander, 1929b; Theischinger, 1996c; Gelhaus, 2009) and probably monophylectic, for instance, on the basis of the modified characters of the radial sector of the wing and the strongly binodulose antennal flagellomeres – apomorphic as compared with the Tipulomorphan ground plan calculated by Ribeiro (2008). Oosterbroek & Theowald (1991) suggested that *Sigmatomera* may represent one of the 'basal lineages' of the family Pediciidae. If so it would be of great age as the Pediciidae is the likely sister group of the rest of the *Tipulomorpha* sensu stricto (Ribeiro, 2008; Petersen *et al*., 2010).

Amphineurus [Family Limoniidae] (Fig. 10)

This genus has four subgenera and over 80 species. *Amphineurus* (*Amphineurus*), with approximately 42 described species, is distributed in southern South America, New Zealand, New Caledonia, Australia and New Guinea. *Amphineurus* (*Rhamphoneurus*) is a southern South American endemic (ten species in Chile and Argentina). The subgenera *A*. (*Nesormosia*) (four species) and *A*. (*Nothormosia*) (18 species) are New Zealand endemics. The Australian species were revised by Theischinger (1994b, 1996b), but there is no recent taxonomic treatment of the species of other regions. Phylogenetic relationships between the included species are unknown and the group is unknown from the fossil record. Edwards (1923) described the New Zealand species known at his time and suggested the genus *Molophilus* as the closest relative of *Amphineurus*.

Aphrophila [Family Limoniidae] (Fig. 11)

Aphrophila includes 19 described species, eight in New Zealand and 11 in southern South America. There are no known fossil species and since the original descriptions of the included species, no comprehensive revision or systematic study has been made.

Zelandomyia [Family Limoniidae] (Fig. 12)

Zelandomyia includes one species from southern South America (Chile) and 11 species in New Zealand, all described by C. P. Alexander between the 1920s and 1940s. The species have never been revised and relationships are unknown. No fossil species is known for this genus.

Leptotarsus (*Leptotarsus*) [Family Tipulidae] (Fig. 13)

The large genus *Leptotarsus* includes over 20 subgenera and over 300 species. The monophyly of the whole genus is doubtful and the group is probably a heterogeneous assemblage of earlier lineages in the family Tipulidae. There are some undescribed *Leptotarsus* fossil species with very long antennae from the Lower Cretaceous Santana Formation (Brazil) (personal observation of the author) and these are among the oldest known Tipulidae.

The subgenus *Leptotarsus* (*Leptotarsus*) includes 17 species in Australia and two species in South America (Chile and Bolivia). The phylogenetic relationships of the included species have never been investigated.

Tonnoiromyia [Family Limoniidae] (Fig. 14)

Tonnoiromyia is a small genus. The three species occurring in Australia were revised by Theischinger (1994b) and the two Neotropical (Chilean) species were described by Alexander (1929a, 1971). Regarding the first discovery of the genus in Chile (with the description of *T. patagonica*), Alexander (1929a: 68) stated that:

The occurrence of a member of this genus, known elsewhere only from Tasmania, was one of the surprises of the Chilean Expedition [. . .] Edwards notes that this species, sometimes associated with *Stibadocerina chilensis* is found in very damp dark places, near small waterfalls or swiftly flowing water.

The group is unknown as fossils and the relationships between the included species, as well as the affinities of the genus, are still obscure.

Limnophilella [Family Limoniidae] (Fig. 15)

Limnophilella includes two species in New Zealand, but is more diverse in the Neotropics, with ten species. The included species, all but one described by Alexander, have never been revised. Gelhaus (2009) treats the taxon as a subgenus of *Austrolimnophila* and suggests it may consist of a highly apomorphic lineage within this group. The genus is unknown from the fossil record.

Dicranomyia (*Zelandoglochina*) [Family Limoniidae] (Fig. 16)

With over 1000 described species in 24 subgenera, *Dicranomyia* is one of the largest genera of crane flies. The genus as a whole has a worldwide distribution. *Dicranomyia* (*Zelandoglochina*) includes 20 Neotropical (Chile and Argentina) and 18 New Zealand species. Edwards (1923) described about half of the New Zealand species. The rest

of the known diversity of the taxon was described by C. P. Alexander in several papers. No fossil species have been ascribed to this particular subgenus, and the relationships between the included species remain unknown.

Conclusions

Previous studies on crane fly distribution patterns (e.g. De Jong, 1998; De Jong *et al.*, 2008) highlighted the high levels of endemism. 'The greater majority of the species and subspecies are restricted to a single biogeographic region, and neighboring biogeographic regions usually share the presence of only a small percentage of species and subspecies' (De Jong *et al.*, 2008).

Charles Paul Alexander, the great specialist of the group, considered the distribution of crane flies as biogeographically meaningful and he interpreted their distributions as strong evidence of direct evolutionary links between the southern continents. This view was strongly rejected by Willi Hennig on the basis of the poor taxonomic and systematic treatment of most taxa. However, although correctly pointing out the need for methodological rigor in systematics, Hennig has, at least in a few cases, underestimated Alexander's capabilities in delineating natural groups. This has been demonstrated by several phylogenetic studies (Vane-Wright, 1967; De Jong, 1989; Ribeiro, 2008, 2009).

The high level of endemicity of the ~700 species of crane flies found exclusively within the limits of the SP-Track is compatible with allopatric differentiation and supports vicariance as the main process behind crane fly disjunctions. However, clearly further studies are essential to provide better diagnosis and definitions of the taxa endemic to the southern hemisphere and to test ideas on their phylogenetic relationships.

As shown in some of the examples treated here, the relationships between some taxa do not agree with the hypothesised hierarchical relationships between the areas (i.e. the temporal sequence of continental breakup). This situation is expected to be found in future studies [for a recent example in the Chironomidae subfamily Orthocladiinae, see Krosch *et al.* (2011)], and caution must be taken when interpreting such cases. First of all, the important role of New Zealand as a critical area in southern hemisphere disjunctions has to be considered, and as demonstrated by Liebherr *et al.* (2011), inferred relationships of New Zealand taxa 'do not support a single hierarchical set of area relationships, corroborating New Zealand's checkered history of area relationships to other austral areas such as southern South America, Australia, and New Caledonia'. Second, some of the groups occurring in the areas can be so old that differentiation could have preceded Late Mesozoic and Cenozoic events. The most recent and comprehensive study of evolutionary patterns in the Diptera (Wiegmann *et al.*, 2011) inferred Tipulomorpha as sister group to the rest of the order, excepting families Deuterophlebiidae and Nymphomyiidae. Molecular-based estimates of divergence times support a Permian origin of the earliest lineages of extant Diptera (including the Tipulomorpha), followed by a rapid diversification in the Triassic (Wiegmann *et al.*, 2011). A considerable portion of trans-Pacific crane flies may be so old that differentiation preceded the final continental breakup.

Distributional patterns of crane flies in the southern hemisphere corroborate a primary hypothesis of biogeographical homology (i.e. shared history) in the South Pacific. The recurrent absence of the taxa dealt with here from typical Gondwanan areas such as India and South Africa are noteworthy. As interpreted here, this is more than just coincidence and suggests the need to address Pacific biogeography with an open mind, acknowledging the existence of patterns more suitably described as trans-Pacific than Gondwanan. The nested subset of distributions in the South Pacific is puzzling, but can be interpreted as evidence of a heterogeneous set of ancestral, prerift distribution ranges in the area.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2011.00594.x

Table S1. Parsimony analysis of endemicity (PAE) data matrix: nexus file, PAST file, TNT file.

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Appendix. Complete authored names of the genus-group taxa cited in the text. The order is alphabetic.

Acracantha Skuse, 1890
Amphineurus Skuse, 1890
Amphineurus (*Nesormosia*) Alexander, 1923
Amphineurus (*Nothormosia*) Alexander, 1923
Amphineurus (*Rhamphoneurus*) Alexander, 1929
Aphrophila Edwards, 1923
Atarba Osten Sacken, 1869
Atarba (*Ischnothrix*) Bigot, 1888
Atypophthalmus Brunetti, 1911
Austrolimnophila Alexander, 1920
Austrotipula Alexander, 1920
Bergrothomyia Alexander, 1928
Chilelimnophila Alexander, 1968
Conosia van der Wulp, 1880
Ctenolimnophila (*Campbellomyia*) Alexander, 1925
Dicranomyia Stephens, 1829
Dicranomyia (*Zelandoglochina*) Alexander, 1924
Discobola Osten Sacken, 1865
Edwardsomyia Alexander, 1929
Elephantomyia Osten Sacken, 1860
Elnoretta Alexander, 1929
Euvaldiviana Alexander, 1981
Gynoplistia Westwood, 1835
Gynoplistia (*Cerozodia*) Westwood, 1835
Gynoplistia (*Dirhipis*) Enderlein, 1917

Gynoplistia (*Xenolimnophila*) Alexander, 1922
Helius Lepeletier and Serville, 1828
Ischnotoma Skuse, 1890
Leptotarsus Guerin-Meneville, 1831
Limnophilella Alexander, 1919
Mesolimnophila Alexander, 1929
Molophilus Curtis, 1833
Notholimnophila Alexander, 1924
Nothophila Alexander, 1922
Paralimnophila Alexander, 1921
Paralimnophila (*Papuaphila*) Alexander, 1947
Rhamphophila Edwards, 1923

Sigmatomera Osten Sacken, 1869
Sigmatomera (Austrolimnobia) Alexander, 1922
Sigmatomera (Eufurina) Alexander, 1946
Stibadocerina Alexander, 1929
Symplecta Meigen, 1830
Tinemyia Hutton, 1900
Tonnoirella Alexander, 1928
Tonnoiromyia Alexander, 1926
Trentepohlia Bigot, 1854
Valdiviana Alexander, 1929
Zelandomyia Alexander, 1923
Zelandotipula Alexander, 1922