

WHERE IN THE WORLD ARE ALL THE TACHINID GENERA?

by James E. O'Hara

Canadian National Collection of Insects, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario, K1A 0C6, Canada; e-mail: james.ohara@agr.gc.ca

INTRODUCTION

Since my earliest studies on tachinids I have been interested in the question of how old are the Tachinidae. I discussed this in a revision of the Siphonini (O'Hara 1989) and concluded that the family must have evolved in the Cenozoic Era because there is no evidence that they appeared any earlier. There are neither Cretaceous fossils nor distribution patterns which suggest that early tachinids existed at the time when Gondwanaland was breaking up. If they had occupied that supercontinent in the Cretaceous, then one might expect to see some tachinid lineages with distributions shared between the southern continents of South America, Africa and Australia, or at least the last two of these to separate, South America and Australia. There may even have been some opportunity for southern dispersal through a more hospitable Antarctica into the early Tertiary (Amorim *et al.* 2009).

A recent "molecular-based time-calibrated phylogeny" of the Diptera by Wiegmann *et al.* (2011) suggested the Schizophora branched off from other cyclorrhaphous flies near the end of the Cretaceous and then underwent a tremendous radiation that "is (together with macrolepidopteran moths) the largest insect radiation in the Tertiary" (p. 5693). In the "Supporting Information" for Wiegmann *et al.* (2011, fig. S3), the Tachinidae were postulated to have separated from their sister-group (the Calliphoridae according to the analysis) about 30 Ma (million years ago) (i.e., during the Oligocene). The fossil record, if taken on face value, sets a minimum age of the Tachinidae at about 44 Ma (i.e., during the Eocene) – but see below!

The "Phylogeny and Evolution of World Tachinidae" project that is discussed by Stireman *et al.* in this issue of *The Tachinid Times* will generate further data relevant to the questions of age and sister group of the Tachinidae. A key goal of the project is the "robust reconstruction of phylogenetic relationships among major tachinid lineages", and this will allow for a bioge-

graphic analysis of tachinid distributions that is not possible outside of a phylogenetic context.

Within this article, I look at distribution patterns of the Tachinidae from the simplistic perspective of genera. The aim is to present the data in visual form and to make a few, mostly obvious, comments about the patterns that are evident. Most of the data are from a list of valid tachinid genera of the world that I first posted on the Internet (along with regional distributions) in 2005 under the title *World Genera of the Tachinidae (Diptera) and their Regional Occurrence*. This document continues to be revised as more papers are published on tachinid systematics and is now in its seventh version (O'Hara 2012). The online data are enhanced here with a new element, that of subfamily placement of each genus.

MATERIALS AND METHODS

The valid genera of Tachinidae and their distributions are listed by O'Hara (2012). The names and distributions were compiled from regional catalogues and updated from all relevant literature published thereafter. A complete list of the catalogues and other sources (ca. 150 publications) that contributed to the list of names and distributions are given in O'Hara (2012).

The data presented here are from a Microsoft Excel spreadsheet that generates the online world list. In addition to names and distributions it also contains tribal and subfamilial placements of genera. Tribes and tribal placements on a world scale are not sufficiently stable to discuss here and also would go beyond the generalizations I want to focus on in this informal newsletter. The "Phylogeny and Evolution of World Tachinidae" project may provide results that can be interpreted within a bio-



geographic context to the tribal level for some lineages of Tachinidae.

Genera are assigned to subfamilies Dexiinae, Exoristinae, Phasiinae and Tachininae or left unplaced. In the last category are the Neotropical genera *Ceratometopa* Townsend, *Marnefia* Cortés, *Parabrachycoma* Blanchard, *Tachinophasia* Townsend, *Tromodesiana* Townsend, and *Xeoprosopa* Townsend and the Australasian genus *Graphia* van der Wulp. Genera that have not been treated universally by modern authors are assigned as follows for the purposes of this article: *Euthera* Loew and *Redtenbacheria* Schiner (both Eutherini) are placed in Dexiinae; *Imitomyia* Townsend and allies (Imitomyiini) are placed in Dexiinae; *Acemya* Robineau-Desvoidy and allies (Acemyini) are placed in Exoristinae; *Palpostoma* Robineau-Desvoidy and allies (Palpostomatini) are placed in Tachininae; *Rondaniooestrus* Villeneuve (sole member of Rondaniooestrini) is placed in Tachininae; and *Strongygaster* Macquart and allies (Strongygastrini) are placed in Phasiinae. In total there are 1516 genera; 1509 are assigned to subfamilies and seven are left unplaced. The Dexiinae and Phasiinae are each generally regarded as monophyletic, Exoristinae may be largely monophyletic, and Tachininae are paraphyletic (e.g., Tschorsnig 1985; also Tachi & Shima 2010 for Exoristinae).

For the sake of simplicity, America north of Mexico is referred to as the Nearctic Region and America south of United States is referred to as the Neotropical Region. The actual boundary between the Nearctic and Neotropical Regions is recognized as a sinuous line through the middle of Mexico. It is difficult to apply this boundary to New World Tachinidae because the distributions of tachinid species in Mexico are so poorly known. The boundary between the Palearctic and Oriental Regions within China is unsettled and I therefore follow Herting and Dely-Draskovits (1993) for the listing of Palearctic genera and Crosskey (1976) for the listing of Oriental genera.

ARE THERE EOCENE FOSSIL TACHINIDAE?

New methods for estimating the age of higher taxa are rejuvenating the question of the age of the Tachinidae. Wiegmann *et al.* (2011) recently suggested an age of about 30 Ma. One way of testing whether this is a realistic estimate is to compare it with the fossil record of Tachinidae. This is quite meager for such a huge family: only 10 described species according to Evenhuis (1994), ranging in age from Holocene to Eocene. Some are in the range of Wiegmann's 30 Ma (Oligocene), and this is true also of some specimens of undescribed species preserved in Dominican amber (Evenhuis 1994). If we accept some or all of these as Tachinidae, then the family is at least as old as the Oligocene.

My interest here is to examine whether the Eocene fossils reputed to be Tachinidae can be confidently identified as belonging to this family. If they can, then a minimum age of Eocene can be accepted for the Tachinidae. If they cannot, then the minimum age of the Tachinidae based on the fossil record is Oligocene.

Evenhuis (1994) listed three tachinids of Eocene age: *Palaeotachina smithii* Townsend (Baltic amber), *Electrotachina smithii* Townsend (Baltic amber), and *Vinculomusca vinculata* (Scudder) (compression fossil from Chagrin Valley, Colorado). The amber speci-



Figure 1. Two flies in Baltic amber from Smith (1868). Based on these drawing and brief notes by Smith, Townsend assigned both to the Tachinidae and named the top one as *Palaeotachina smithii* Townsend, 1921 and the bottom one as *Electrotachina smithii* Townsend, 1938.

mens date to 44.1 ± 1.1 Ma according to Engel's (2001) review of Baltic amber. To my knowledge, no one has doubted that Townsend's Eocene fossil taxa belong to the Tachinidae. However, just a cursory examination of the evidence is enough to make one question the familial placements of these taxa.

Zaddach (1868) published on the origin and history of the amber of "Samland", a famous source area for Baltic amber. The editors of the journal in which Zaddach's paper appeared inserted a plate of amber fossils after the paper "for the benefit of such students as desire to inform themselves more fully concerning the natural history of Amber" (p. 183). The

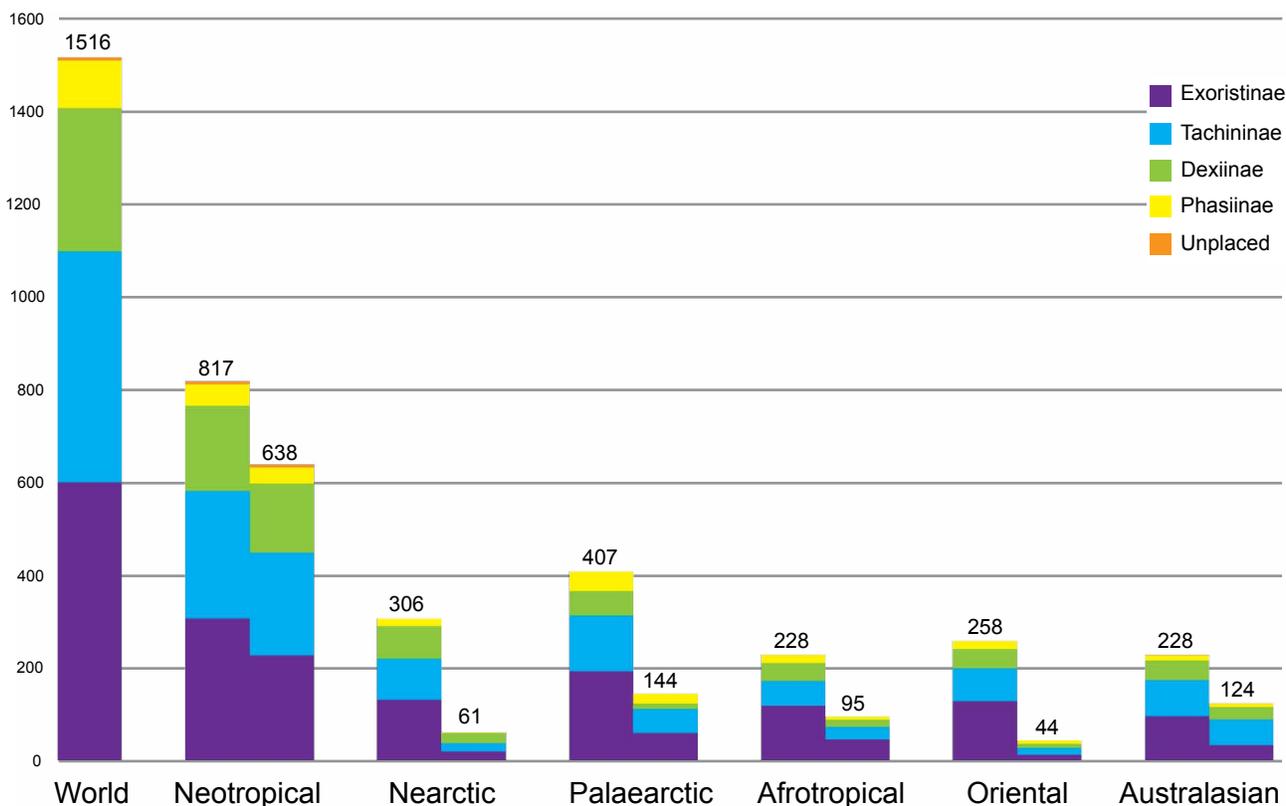


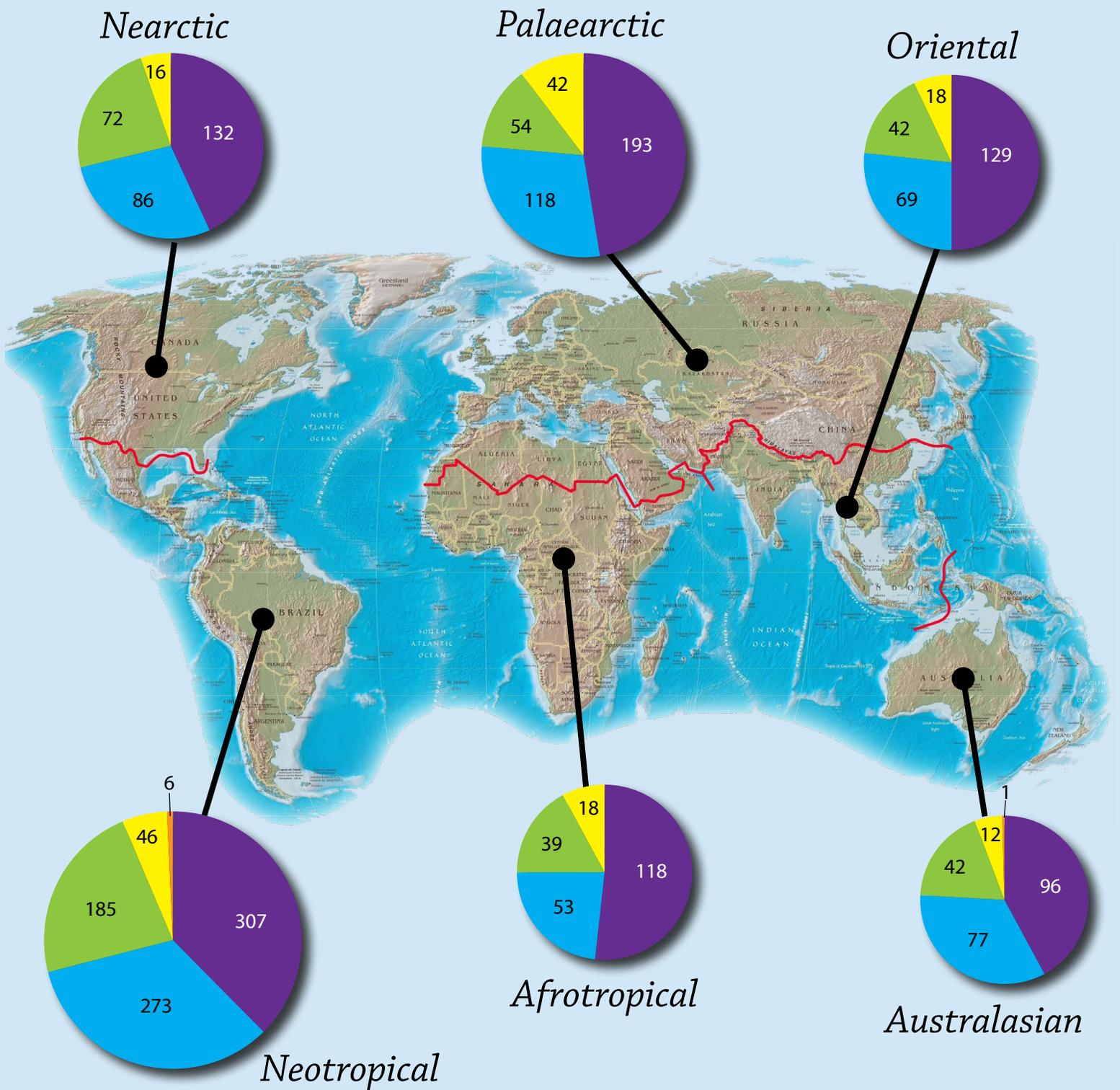
Figure 2. The leftmost bar in the graph shows the number of valid tachinid genera in the world. Bars for each region show the total number of genera on the left and number of endemic genera on the right. Colours represent the four tachinid sub-families and unplaced genera.

plate illustrates 11 fossils from the British Museum and Frederick Smith of that institution provided a caption for each (plate and captions cited here as Smith 1868). Three flies are depicted in the plate, of which two are shown here in Fig. 1 in their original position of one above the other (numbered on the plate as 2 and 5). This reproduction of a portion of the plate is from a PDF available from the Biodiversity Heritage Library (<http://www.biodiversitylibrary.org/>). Although the reproduction is poor, it appears as though the figures were intended to show the general aspect of fossils in amber rather than the precise anatomical features of the material illustrated. This is borne out by a remark from the editors that the plate “will convey some idea of the organic remains usually found in this fossil resin” (p. 183). Smith (1868) was able to examine the fossils and wrote of his fig. 2: “A Dipterous Insect belonging to the European genus *Echinomyia*”. Of his fig. 5, Smith wrote: “A Dipterous Insect belonging to a new genus of Muscidae, allied to the European genus *Tachinus*”. Townsend (1921), apparently without seeing the fossil and relying upon the drawing in Fig. 1 and Smith’s brief note, described the fly in Smith’s fig. 2 as a new genus and species of “Larvaevorini or allied tribes” under the name *Palaeotachina smithii*. Years later, Townsend (1938) described the fly in Smith’s fig. 5 as a new genus

and species “probably [of] exoristid or tachinid stock” under the name *Electrotachina smithii*, again presumably without seeing the actual specimen. The strongest evidence that these taxa might belong to the Tachinidae is the identifications by Smith (a non-specialist on the Diptera) who saw the specimens; even a specialist like Townsend would not be able to conclusively identify the taxa from the drawings published of them.

The other so-called tachinid of Eocene origin is *Vinculomusca vinculata* (Scudder). This species was originally described by Scudder (1877) in the genus *Musca* based on compression fossils of several empty larval skins. Townsend (1938) transferred the species to his new genus *Vinculomusca* and declared it of “apparently exoristid or tachinid stock”. There is no reason to suppose that the larvae were arthropod parasitoids, which one would expect of tachinid larvae.

This cursory review of reputed Eocene Tachinidae is enough to cast doubt on the familial placements of these fossil Diptera. Until such time as the type specimens can be examined it is best to treat the familial placements of these taxa as questionable. If these taxa cannot be confirmed as Tachinidae, then there is no credible proof that the tachinid lineage existed in the Eocene. It could have, but there is no fossil evidence in support of it.



LEGEND

- Exoristinae
- Tachininae
- Dexiinae
- Phasiinae
- Unplaced

Figure 3. The number of valid genera of Tachinidae in each biogeographic region of the world is shown in proportionally-sized pie charts. The number of genera per subfamily is shown within each pie chart. The total number of genera for the world is 1516.

Understanding the historical biogeography of tachinid flies is hampered by this sketchy knowledge of their age, as it is by the lack of a well-supported phylogeny. I leave open the question of when the Tachinidae began their diversification in the Tertiary and turn my attention to a review of the present distributions of the genera of world Tachinidae.

DISTRIBUTION OF TACHINID GENERA

Genera per region

The total number of extant and valid genera of Tachinidae in the world (currently 1516) and number of genera per region are shown graphically in Fig. 2 with different colours representing the tachinid subfamilies. A second bar to the right of the first for each region shows the number of endemic genera (see discussion below).

The number of genera per region is shown again in Fig. 3 using pie charts. These charts are proportionally-sized with their volumes representing the number of genera per region, thereby visually depicting differences between regions.

Without getting too speculative about what the numbers might mean, there are some patterns that I think are evident:

1) The dominant subfamily in the world is the Exoristinae with 601 genera.

2) Regardless of where tachinid lineages evolved or what hosts are parasitized, the same order from largest to smallest subfamily is repeated in each of the six biogeographic regions: Exoristinae, Tachininae, Dexiinae and Phasiinae.

3) The Neotropical Region leads the world with 817 genera, twice the number of any other region and fully 54% of the world's genera. There are, however, extenuating circumstances. Townsend, for example, named an extraordinary number of genera from the Neotropics and was a renowned "splitter". A careful reappraisal of his Neotropical genera will lower their number considerably. However, the number will creep up again (but probably not to where it is today) because the Neotropics has a vast number of undescribed species in addition to its 3000-odd current species and some of these will need new genera. The Neotropics is blessed with an unusually diverse tachinid fauna and I suspect the region will always be dominant in number of genera despite

the downsizing that will occur as broader generic limits are set for existing genera.

4) The Palaearctic Region is comfortably in second place with 407 genera. The simplest explanation for this is the immense size of the region, its physiographic diversity, and its physical connection with two other regions (Afrotropical and Oriental) and former connection with another (Nearctic). The fauna of the Palaearctic Region is the best known in the world, particularly in the West Palaearctic subregion, Russian Far East, and Japan; Palaearctic China and mountainous areas of Central Asia are less well known.

5) The most peculiar aspect of the Australasian tachinid fauna in my view is how little it differs in number of genera from the Oriental Region. It also harbours much greater diversity than current catalogues would suggest (e.g., O'Hara *et al.* 2004). One might expect that the isolated nature of Australia throughout most of the Tertiary would have resulted in a depauperate fauna if tachinids evolved elsewhere. Is it possible that tachinids have had a long history in Australia? Or, did they disperse from elsewhere across water barriers more successfully and earlier than the megafauna?

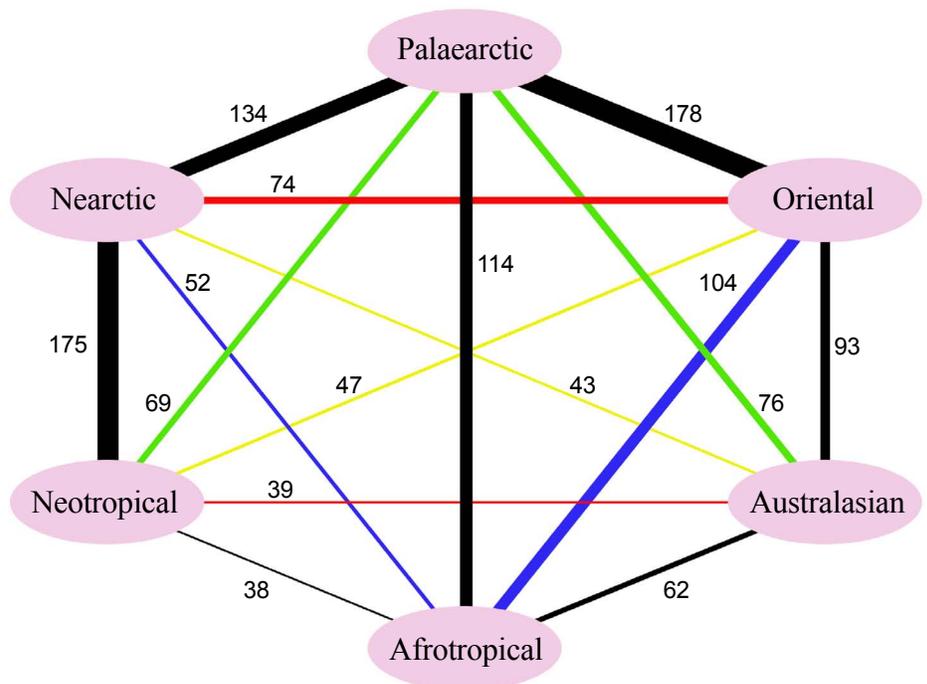


Figure 4. The number of genera shared between two regions is shown with proportionally-sized lines between the six biogeographic regions. The greatest number of genera is shared between the Palaearctic–Oriental regions and Nearctic–Neotropical regions, respectively.

Endemic genera

The number of endemic genera per region is shown in Fig. 2. The Neotropical Region is the overwhelming leader with 638 genera, which is 78% of all Neotropical genera. This is an extraordinary figure but is tempered by the fact that many of the genera of the region are too restricted in their concepts (as discussed in the previous section). Numerous genera will eventually be merged with other Neotropical genera or with genera known from the Nearctic Region (as already done for a large portion of the *Blondeliini* by Wood 1985). Be this as it may, there is a great deal of endemism in the Neotropical tachinid fauna.

The Palaearctic Region has the next highest number of endemic genera with 144 (35% of total), but this is a little misleading because the total fauna is very large. In terms of the proportion of endemic genera to total number of genera, both the Australasian Region (with 124 endemic genera and 54% endemism) and the Afrotropical Region (with 95 endemic genera and 42% endemism) are higher than the Palaearctic Region.

Genera shared between two regions

The greatest number of genera is shared between the Palaearctic–Oriental Regions and Nearctic–Neotropical Regions, with 178 and 175 shared genera, respectively (Fig. 4). It is not surprisingly that many genera are shared between the Palaearctic and Oriental Regions given that the boundary between them is long and in places (e.g., China) exceptionally transitional in nature. The boundary used here between the Nearctic and Neotropical Regions is an arbitrary one and may account in part for the high number of shared genera, but what is not shown by the numbers is the high number of genera that are shared between North and South America. I suspect that the “Great American Biotic Interchange” that is recognized for mammals and started with the emergence of the Panamanian land bridge a few million years ago was not so much a factor for tachinids; there must have been significant interchange prior to this time, perhaps over some sort of “filter bridge” (e.g., O’Hara 1989).

There is quite a significant sharing of genera (134) between the Nearctic and Palaearctic Regions. Since these regions are currently separated by a significant water barrier, periodic land connections across the Bering Strait and the North Atlantic during the Cenozoic Era are believed to have acted as faunal corridors for many organisms, including tachinids.

The Afrotropical Region shares genera mostly with the Palaearctic and Oriental Regions (114 and 104

genera, respectively). It may seem odd that the number of genera shared between the Afrotropics and each of these two regions is so similar. After all, the Palaearctic and Afrotropical Regions are broadly contiguous and the Sahara Desert did not begin development (and hence become a barrier) until the Pliocene, and continued to experience wet-dry cycles thereafter (Le Houérou 1997, Micheels *et al.* 2009). In contrast, the Oriental and Afrotropical Regions are barely joined and probably experienced less faunal interchange during the Neogene (but the timing and biogeographic effects of the Indian–Asian collision is still controversial, see Li *et al.* 2013). Yet, there is another factor that helps to explain the high relative similarity between the tachinid genera of the Oriental and Afrotropical Regions: 88 of 104 genera shared between them are also shared with the Palaearctic Region. Only 11 genera are uniquely shared between the Oriental and Afrotropical Regions compared with 21 genera uniquely shared between the Palaearctic and Afrotropical Regions.

The three southernmost regions, the Neotropical, Afrotropical and Australasian, have few genera shared between them and most are shared also with other regions. It is commonly assumed, but has yet to be corroborated by a well-supported phylogenetic tree, that this pattern does not support the existence of a noticeable tachinid fauna before the breakup of Gondwanaland.

Genera of worldwide distributions

Assuming that genera are correctly recognized in the six biogeographic regions (which may not be true in all cases), there are only 25 genera (1.6% of the total) of Tachinidae recorded from all regions. Twelve belong to the Exoristinae:

Apomyia Robineau-Desvoidy, *Carcelia* Robineau-Desvoidy, *Ceracia* Rondani, *Chetogena* Rondani, *Drino* Robineau-Desvoidy, *Gonia* Meigen, *Lydella* Robineau-Desvoidy, *Nemorilla* Rondani, *Nilea* Robineau-Desvoidy, *Sisyropa* Brauer & Bergenstamm, *Trigonospila* Pokorný, and *Winthemia* Robineau-Desvoidy.

Six belong to the Tachininae:

Actia Robineau-Desvoidy, *Ceromya* Robineau-Desvoidy, *Leskia* Robineau-Desvoidy, *Linnaemya* Robineau-Desvoidy, *Microphthalma* Macquart, and *Siphona* Meigen.

Five belong to the Dexiinae:

Billaea Robineau-Desvoidy, *Campylocheta* Rondani, *Euthera* Loew, *Thelaira* Robineau-Desvoidy, and *Voria* Robineau-Desvoidy.

Two belong to the Phasiinae:

Cylindromyia Meigen and *Phasia* Latreille.

ACKNOWLEDGEMENTS

I am grateful for the assistance of summer student Natasha MacDonald for adding data about the affinities of tachinid genera into an Excel spreadsheet containing the names of all valid genera, and for preparing preliminary versions of bar graphs and pie charts for my perusal. I thank Shannon Henderson for preparing Fig. 2 and completing my early draft of Fig. 3. Neal Evenhuis kindly reviewed this article and offered helpful suggestions, especially concerning the fossil record of Tachinidae.

REFERENCES

- Amorim, D.S., Santos, C.M.D. & Oliveira, S.S. de (2009) Allochronic taxa as an alternative model to explain circumantarctic disjunctions. *Systematic Entomology*, 34, 2–9.
- Crosskey, R.W. (1976) A taxonomic conspectus of the Tachinidae (Diptera) of the Oriental Region. *Bulletin of the British Museum (Natural History). Entomology Supplement*, 26, 357 pp.
- Engel, M.S. (2001) A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History*, 259, 192 pp.
- Evenhuis, N.L. (1994) *Catalogue of the fossil flies of the world (Insecta: Diptera)*. Backhuys Publishers, Leiden. 600 pp.
- Herting, B. & Dely-Draskovits, Á. (1993) Family Tachinidae. Pp. 118–458. In: Soós, Á. & Papp, L. (eds.), *Catalogue of Palaearctic Diptera*. Volume 13. Anthomyiidae—Tachinidae. Hungarian Natural History Museum, Budapest. 624 pp.
- Le Houérou, H.N. (1997) Climate, flora and fauna changes in the Sahara over the past 500 million years. *Journal of Arid Environments*, 37, 619–647.
- Li, J.-T., Li, Y., Klaus, S., Rao, D.-Q., Hillis, D.M. & Zhang, Y.-P. (2013) Diversification of rhacophorid frogs provides evidence for accelerated faunal exchange between India and Eurasia during the Oligocene. *Proceedings of the National Academy of Sciences of the United States of America*, PNAS Early Edition, 6 pp. [doi: 10.1073/pnas.1300881110]
- Micheels, A., Eronen, J. & Mosbrugger, V. (2009) The Late Miocene climate response to a modern Sahara desert. *Global and Planetary Change*, 67, 193–204.
- O'Hara, J.E. (1989) Systematics of the genus group taxa of the Siphonini (Diptera: Tachinidae). *Quaestiones Entomologicae*, 25, 1–229.
- O'Hara, J.E. (2012) *World genera of the Tachinidae (Diptera) and their regional occurrence*. Version 7.0. PDF document, 75 pp. Available from: http://www.nadsdiptera.org/Tach/Genera/Gentach_ver7.pdf (accessed [11 February 2013]).
- O'Hara, J.E., Skevington, J.H. & Hansen, D.E. (2004) A reappraisal of tachinid diversity in Carnarvon N.P., Australia, and estimation of the size of the Australian Tachinidae fauna. *The Tachinid Times*, 17, 8–10.
- Scudder, S.H. (1877) The first discovered traces of fossil insects in the American tertiaries. *Bulletin of the Geological and Geographical Survey of the Territories*, 3, 741–762.
- Smith, F. (1868) Explanation of the plate of organic remains found in amber. *Quarterly Journal of Science*, 5, 183–184 + pl. 18.
- Tachi, T. & Shima, H. (2010) Molecular phylogeny of the subfamily Exoristinae (Diptera, Tachinidae), with discussions on the evolutionary history of female oviposition strategy. *Systematic Entomology*, 35, 148–163.
- Townsend, C.H.T. (1921). Some new muscoid genera ancient and recent. *Insector Inscitiae Menstruus*, 9, 132–134.
- Townsend, C.H.T. (1938) Five new genera of fossil Oestromuscaria. (Diptera). *Entomological News*, 49, 166–167.
- Tschorsnig, H.-P. (1985) Taxonomie forstlich wichtiger Parasiten: Untersuchungen zur Struktur des männlichen Postabdomens der Raupenfliegen (Diptera, Tachinidae). *Stuttgarter Beiträge zur Naturkunde. Serie A (Biologie)*, 383, 137 pp.
- Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.B., Kim, J.-W., Lambkin, C., Bertone, M.A., Casse, B.K., Bayless, K.M., Heimberg, A.M., Wheeler, B.M., Peterson, K.J., Pape, T., Sinclair, B.J., Skevington, J.H., Blagoderov, V., Caravas, J., Kutty, S.N., Schmidt-Ott, U., Kampmeier, G.E., Thompson, F.C., Grimaldi, D.A., Beckenbach, A.T., Courtney, G.W., Friedrich, M., Meier, R. & Yeates, D.K. (2011) Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 5690–5695.
- Wood, D.M. (1985) A taxonomic conspectus of the Blondeliini of North and Central America and the West Indies (Diptera: Tachinidae). *Memoirs of the Entomological Society of Canada*, 132, 130 pp.
- Zaddach, G. (1868) Amber; its origin and history, as illustrated by the geology of Samland. *Quarterly Journal of Science*, 5, 167–183 + [1] pl.