The historical biogeography of *Simulium* Latreille subgenera of the Neotropical, Afrotropical, and Australian-oriental Regions is reconstructed applying dispersal-vicariance analysis. The results suggest that the genus originated within an area represented by Pangea. This places the origin for the genus in the middle of the Jurassic Period (180-160 Mya).

INTRODUCTION

*Simulium* Latreille, 1802, is the most speciose simulid genus, comprising almost 75% of the described species of the family Simuliidae (Crosskey & Howard 1997). The genus occurs in all biogeographical regions, although each subgenus is confined to one or more regions. The first uncontroversial fossil assigned to the family is a member of the tribe Prosimuliini (*sensu* Currie 1988), from the Jurassic/Cretaceous transition, namely: *Kovalevnyia lacrimosa* Kalugina, 1991, from Siberia (Currie & Grimaldi 2000). The oldest Southern Hemisphere fossil originates from the Cretaceous Koonwarra fossil beds of Australia (135 Mya), and Crosskey & Howard (1997) assigned this species to the African genus *Paracnephia* Rubtsov, 1962, indicating a Gondwanian origin. Craig et al. (2001) presented a biogeographic analysis of the subgenus *S.* (*Inseliellum*) Rubtsov, 1974, and suggested that *Simulium* 'evolved' prior to the separation of New Zealand from Australia/Antarctica (between 80-60 Mya). Crosskey (1990: 58) believed that the family was widespread in Pangea and dated the origin of the family to at least the early Jurassic (200-175 Mya). He considered, however, dispersal to be the main mechanism explaining the current distribution patterns of simulid genera and subgenera without vicariance playing a crucial rôle.

He also proposed that Antarctica would have been habitable by simulids at that time, and therefore the continent could have acted as a bridge between Australia and New Zealand, and South America.

Coscarón & Coscarón-Arias (1995) presented a preliminary biogeographical analysis of the neotropical simulid fauna, delimiting 16 areas of endemism. These provinces, in a slightly modified form, were later used in a biogeographical analysis by Miranda-Esquivel (2001). In that study, the rôle of dispersal in the distribution of neotropical simulid subgenera was evaluated. Eliminating the commonest dispersal events, the general area cladogram was found to be congruent with terrestrial biota, where two sub-regions arise: the Neotropical Subregion (*sensu stricto*) (Cerrado, SE Brasil, Guyana and Amazonia, which is synonymous with the Guyano-Brasilian Region of Jeannel (1942)), and the Andean Sub-region, which is equivalent to the Andean Region proposed by Morrone (1996). Pacifica and the Mesoamerican Mountains were placed apart from the main Neotropical Region clade (*vide* Figure 1). Miranda-Esquivel & Coscarón (submitted) present a preliminary attempt at a cladistic analysis of the genus at the subgeneric level for the Neotropical/Afrotropical/Australian-oriental Regions.
Event-based methods have increased in importance in historical biogeographic studies over recent years. Unlike most other pattern-based methods, event-based methods postulate explicit models of processes that effect the geographic distribution of living organisms. In this context, different process types (i.e. vicariance, dispersal, extinction) are identified, and costs are assigned in accordance to the model (Ronquist 1996, 1997, 2002). Dispersal-vicariance analysis (Ronquist 1997) allows for the reconstruction of ancestral distributions, maximises vicariance events, and minimises dispersal and extinction events, but unlike pattern-based methods of cladistic biogeography, it allows non-hierarchical area relationships. This method has been widely implemented to evaluate dispersal-vicariance events (Donato et al. 2003; Miranda-Esquivel 2001; Voelker 2002; Xiang & Soltis 2001; Zink et al. 2000), and to reconstruct the ancestral area (Anderson 2000; Burns et al. 2002; Davis et al. 2002a, 2002b; Långtröm 2002).

The purpose of this paper is to analyse distributional patterns of the subgenera of Simulium within the framework of historical biogeography event-based methods by applying dispersal-biogeography analysis (Ronquist 1997). Here an attempt is made to discern the ancestral areas of the Gondwanian components of the genus Simulium. This is a preliminary approach, and a more refined analysis, conducted at the species-group level, would ultimately be more informative.

**METHODS**

In order to reconstruct the ancestral distributions of the subgenera of Simulium, the program DIVA 1.2 (Ronquist 1996) is used, and a heuristic search using dispersal-vicariance optimisation is applied (Ronquist 1997). DIVA infers the ancestral distribution for a taxon and calculates the frequencies of vicariance and dispersal events among and between the areas under consideration. In order to do so, the program constructs a three-dimensional cost matrix derived from a simple biogeographic model and the phylogenetic information encoded on the taxon cladogram (Ronquist 1997). Although some other pattern approaches could be used, e.g. treefitter (Ronquist 2001, 2002) and Secondary BPA (Brooks 1990), DIVA requires the least number of assumptions (contra Weller & Brooks 2001). The distribution pattern of Simulium subgenera is analysed using the phylogeny proposed by Miranda-Esquivel & Coscarón (submitted) (Figure 2). The original cladogram is fully resolved, although that illustrated in Figure 2 has some polytomies due to uncertainty in some parts of the cladogram. The current analysis was conducted using subgenera as terminals. Alternative topologies found in Miranda-Esquivel & Coscarón (submitted), using different concavity values in PIWE (vide Goloboff 1993, 1998), are also analysed. For the subgenera S. (Gomphostilbia) Enderlein, 1921, S. (Nevermannia) Enderlein, 1921, and S. (Morops) Enderlein, 1930, the analysis of Otsuka et al. (2001) is also used (Figure 3).

In total, 13 areas are included, and in the neotropics, seven main provinces of endemism are
considered, all defined in previous biogeographic publications (Coscarón & Coscarón-Arias 1995). For Africa the classical Wallacian sub-regions are used (Brown & Lomolino 1998). For the sake of this analysis, the Nearctic and Palaearctic Regions are included, and the Australasian and Oriental Regions are considered as a single biogeographic region. This is not a novel approach, the combined Australian-oriental Region, for example, was used by Ward (2001).


To infer the age of a clade, the age of vicariance events, as derived from geological data, is used following Cracraft (2001). To estimate the divergence time of clades, the data from the ‘plates project’ was used (Anon 2002). While other methods to establish divergence time exist (e.g. Huelsenbeck & Imennov 2002), the molecular database for Simulium is currently insufficient to attempt such analyses.
RESULTS & DISCUSSION

The solutions calculated here require 65 or 66 dispersals and 45 speciation events, suggesting that current distribution patterns are highly influenced by dispersal events. Most dispersal events were intra-continental, whereas vicariance explains most of the inter-continental patterns. Analyses with the same phylogenetic topologies, but with the biogeographical zones reduced to a continental scale (Neotropical, Afrotropical, Nearctic, Palaearctic, and the Australian-oriental Regions), yielded only 12 dispersal events. These dispersal events could further be an artefact of uncertainty in the phylogeny, given different optimisations (vide Figure 4). Dispersal is a critical process in the cladogenesis of most taxa (Zink et al. 2000) and has also played a critical rôle in the biogeography of Simulium spp. (Craig et al. 2001; Miranda-Esquivel 2001); the results here, however, suggest that vicariance is the most important cause of divergence at the subgeneric level.

This analysis found that the Central Rainforest + Savanna was the ancestral area for the afrotropical clade: S. (Lewisellum) Crosskey, 1969 + S. (Phoretomyia) Crosskey, 1969. This clade is recovered in all the phylogenetic analyses. It is a young clade that may be dated as early as the post Cretaceous or Tertiary. The sister-group to this taxon may be S. (Psilozia) vittatum Enderlein, 1936, as suggested by some of these analyses, but this proposed relationship infers an unlikely vicariance or dispersal event. For the clade S. (Pomerojellum) Rubtsov, 1962 + S. (Meilloniellum) Rubtsov, 1962 + S. (Nevermannia) ruficorne-group, the ancestral area is also the Central Rainforest + Savanna, and this is also a recent divergence. African and South American Prosimulini (sensu Coscarón 1991) may also have had a Godwanian distribution. Neotropical Araucnephia Wygodzinsky & Coscarón, 1973, and

Figure 3. Cladogram after Otsuka et al. (2001). This is an alternative solution to the Australian-oriental. Taxa abbreviation: S. = Simulium; N. = Nevermannia.

Austrosimulium Tonnoir, 1925 + Paraustrosimulium Wygodzinsky & Coscarón, 1962, represent the most basal clade in the tribe Simuliini. These two genera were considered to be sister-groups by Wygodzinsky & Coscarón (1962). Dumbleton (1963) suggested that Austrosimulium was derived from Gigantodax Enderlein, 1925, and that they both originated in South America or in Antarctica. Crosskey (1987) did not include both taxa in the same clade. According to the present analysis, the ancestral area for Austrosimulium + Paraustrosimulium is Australia + Subantarctic province, indicating a clear Gondwanian relationship with a southern ocean baseline (Craw et al. 1999). Many southern South America/Australia events have been dated as late Cretaceous, because the isolation between Australia and southern South America began with opening of the Drake Passage about 36 Mya (Pascual 1998), and this isolation increased with the formation of ice caps on Antarctica (Crosskey 1990). Placing the origin of the ice caps at the middle Miocene (13-10 Mya), the basal position of the clade must be prior to this date, and could be as early as the opening of the South Atlantic circa 135 Mya. In agreement with Crosskey (1990), the taxon inhabited Antarctica. Lutzsimulium hirticosta Lutz, 1909, could be the sister-group to the previous clade. This sister-group relationship reinforces the idea of a Gondwanian relationship and does not influence the estimated divergence time.
Araucnephiodes Wygodzinsky & Coscarón, 1973, are phenotypically more similar to the South African Paracnephia (Paracnephia) Rubtsov, 1962, than to any other neotropical genus (Coscarón & Coscarón-Arias 2002), and Paracnephia has a clear Gondwanian origin (Crosskey & Howard 1997).

The ancestral area for the Australian-oriental clade *S. (Inseliellum), S. (Morops), S. (Gomphostilbia)* and the *S. (Nevermannia) loutetense-group* is the Australian-Oriental Region + Africa. This could be a recent divergence. Craig et al. (2001) considered the divergence for *S. (Gomphostilbia), S. (Inseliellum), S. (Morops)* and *S. (Wallacellum)* Takaoka, 1983, to be 20 Mya as a dispersal across SE Asia; while *S. (Hebridosimulium)* Grenier & Rageau, 1961, dispersed to Fiji and Vanuatu circa 10-6 Mya. Otsuka et al. (2001), applied molecular data to analyse the Australian-oriental clade (Figure 3), but did not include *S. (Inseliellum), S. (Hebridosimulium)* and *S. (Wallacellum).* This finding suggests that *S. (Nevermannia) feuerborni-group* could have a palaeartic or oriental origin. The divergence of the Australian-oriental clade that includes both subgroups (Africa + Australian-oriental clades) may be placed in the lower Cretaceous. This pattern, with an Indian Ocean baseline (Craw et al. 1999) joining the Africa + Australian-Oriental Regions, has been found in other analyses. For example, Ward (2001) found an African origin for the genus *Tetraponera* Smith, 1852, and four independent origins for the Australian-oriental clades. He placed the divergence time for *Tetraponera* in the Cretaceous. Holloway & Hall (1998) showed a similar pattern with some groups of Lepidoptera (Troidini, Callidulidae, Uranidae and Castniidae), although there was no common pattern for the four taxa.
Neotropical *Simulium* subgenera are divided into three subclades. The first clade, *S.* (*Ectenmassipi*) Enderlein, 1934, *S.* (*Psilopelmia*) Enderlein, 1934, and *S.* (*Chirostilbia*) Enderlein, 1921, represents a well-supported node (Coscarón 1987), for which the ancestral area was found to be the entire Neotropical Sub-region, excluding Deserts and Puna. Coscarón et al. (1996) analysis suggests that the nearctic component of the *S.* (*Psilopelmia*) clade might be a basal divergence in the subgenus and that this divergence within the genus is rather recent, though they did not suggest a divergence time. The sister-group to *S.* (*Ectenmassipi*), *S.* (*Psilopelmia*), and *S.* (*Chirostilbia*) is *S.* (*Psaroniocompsa sensu lato*) Enderlein, 1934, *S.* (*Inaequalium*) Coscarón & Wygodzinsky, 1984, *S.* (*Aspathia*) Enderlein, 1935, and *S.* (*Notulepria*) Enderlein, 1930. This research supports the hypothesis that the latter clade is neotropical, with Mesoamerica (Caribbean + Pacifica + Mesoamerican Mountains) as the ancestral area. It is also a recent divergence.

In the neotropical realm, *S.* *blancasi*-group + *S.* (*Pternaspatha*) Enderlein, 1930, form a well-established clade (Coscarón 1987; Coscarón & Coscarón-Arias 1996; Miranda-Esquivel & Coscarón submitted). Its ancestral area is Desert/Puna. If *S.* (*Afrosimulium*) Crosskey, 1969, is considered as the sister-group to this taxon, as suggested in some of these optimisations (Figure 4), the ancestral area for this clade (*Afrosimulium* + (*blancasi*-group + *Pternaspatha*)) is South Africa - Desert/Puna. This indicates an ancient origin for the clade in the early Cretaceous (circa 110 Mya) or even late Jurassic, before the separation of southern Gondwana and the formation of the southern Atlantic Ocean (Pitman et al. 1993). The weather in the middle America-south and central Africa, from the Volgian onwards, became a winter-wet zone, after a longer desert zone period during the Jurassic (Rees et al. 2000). This shall undoubtedly be regarded as a rather controversial date, as the oldest known fossil for the family is a *Prosimulium*-like genus that has been dated as Jurassic/Cretaceous, and because Prosimulini *sensu* Currie (1988) is older than Simulini. A suggested solution to solve the too early date is a dispersal event across a narrow proto-Atlantic. This solution could be possible, but no longer than 100 Mya. There is no evidence of extant species belonging to the clade (*Afrosimulium* + (*blancasi*-group + *Pternaspatha*)) in the southern Atlantic islands. The alternative solution, found with other optimisations, is for *S.* (*Afrosimulium*) to be placed as the sister-group of *S.* (*Methomphalus*) Enderlein, 1935, and the ancestral area for this taxon (*Afrosimulium* + *Methomphalus*) would be South Africa + Savanna.

The clade *S.* (*Thyropelma*) Enderlein, 1934, *S.* (*Trichodagmia*) Enderlein, 1934, *S.* (*Freemanellum*) Crosskey, 1969, *S.* (*Anasolen*) Enderlein, 1930, *S.* (*Xenosimulium*) Crosskey, 1969, and *S.* (*Hemicnetha*) Enderlein, 1934, is well supported (Miranda-Esquivel & Coscarón 2001), which falsifies the hypothesis that all neotropical *Simulium* spp. form a monophyletic clade (Coscarón 1987). These results show that the ancestral area of *S.* (*Thyropelma*) + *S.* (*Trichodagmia*) is Amazonia *sensu latissimo* (Guyana + Amazonia + Cerrado + SE Brasil), while the ancestral area for the whole clade (*Thyropelma* + *Trichodagmia* + *Freemanellum* + *Anasolen* + *Xenosimulium* + *Hemicnetha*) is Amazonia s.l. + Africa. All subgenera are found exclusively in Africa or South America, suggesting that the vicariance event separating them was in the early Cretaceous, circa 100 Mya, or as early as the beginning of the Cretaceous (Anon 2002; Cracraft 2001). Since the late Jurassic, the weather in the Amazonia-Africa junction has been summer-wet (Rees et al. 2000). The African subgenera *S.* (*Methomphalus*) together with *S.* (*Edwarssellum*) Enderlein, 1921, and the *S.* (*Byssodon*) *griseicolle*-group are basal to the Gondwanian clade (*vide* Figure 2). This result could infer a Gondwanian origin to these subgenera. According to these results, the ancestral area of *S.* (*Edwarssellum*) + *S.* (*Byssodon*) *griseicolle*-group could be Africa or the palaeartic. It is therefore difficult to explain the distribution of *S.* (*Byssodon*) Enderlein, 1925. It could be a palaeartic subgenus with a broad dispersal, or a non-monophyletic taxon such as *S.* (*Nevermannia*), where various components are found in different regions.

The neotropical, *Simulium ovidoir* species-group is a problematic taxon. Some of these results suggest a sister-group relationship with *S.* (*Ectenmassipi*) + *S.* (*Psilopelmia*) + *S.* (*Chirostilbia*) (Coscarón 1987), or alternately a sister-group with *Hemicnetha* (Ramírez-Pérez 1971). The affinities are still unclear, but neither of the two possible solutions
alter the optimisation of the ancestral area. The Nearctic subgenus *S.* (Psilozia) is placed as a basal taxon in this analysis, and this may indicate a ‘remote’ relationship to the Nearctic/Palaearctic *Simulium* fauna. This hypothesis could be tested only with a phylogenetic analysis that includes all Nearctic and Palaearctic subgenera.

The Neotropical and the Afrotropical Regions are complex areas that exhibit different affinities (Figure 5). The Neotropical Sub-region is closest in simulid phylogenetic similarity to central Africa [the Atlantic Ocean baseline, Craw et al. (1999)]. This pattern is evident in the *S. (Thysopelma), S. (Trichodagmia), S. (Freemanellum), S. (Anasolen) and S. (Xenosimulium)* clade. The Andean Sub-region is related to the Australian-Oriental Region [the southern Ocean baseline, Craw et al. (1999)]. This pattern is present in the divergence between the sister taxa *Austrostomilium* and *Paraustrostomilium.* Africa is also related to the Australian-Oriental Region [the Indian Ocean baseline, Craw et al. (1999)]. This pattern is evident in the divergence of the sister taxa *S. (Inseliellum), S. (Morops), S. (Gomphostilbia), and S. (Nevermannia) lautetense,* where the basal African taxon *S. (Nevermannia) lautetense* is related to the Australian-oriental clade *S. (Inseliellum), S. (Morops)* and *S. (Gomphostilbia).*

The area cladogram presented here ((Australian-Oriental, Southern South America) + ((Africa, Australian-Oriental) + ((Africa, Amazonia), South America))), do not completely agree with the general pattern proposed for Gondwanian clades (Linder & Crisp 1995). Although, some sister areas do agree, such as Africa + Oriental, and Southern South America + Australia. The only difference lies in the basal divergence between Southern South America + Australia. The interpretation is that this divergence is dated towards the time of the opening of the South Atlantic 135 Mya, suggesting a connection via Antarctica. This hypothesis is

---

**Figure 5.** Distributional patterns for neotropical, afrotropical and Australian-oriental *Simulium* Latreille subgenera. Some additional genera have been included to illustrate general affinities (after Crosskey (1990)). Dates from Cracraft (2001) and the ‘Plates project’ (Anon 2002).
different than that proposed by Crosskey (1990), and it is in better agreement with the general area cladogram proposed by Linder & Crisp (1995). Nonetheless, the divergence from the general pattern may also be assigned to dispersal. These results are not unique in differing from the general pattern, incongruence has been found with other groups (e.g. Edgecombe et al. 2002).

Not surprisingly, the ancestral area for the whole clade under analysis is a zone that includes all the areas considered. Such a wide distribution means that *Simulium* is older than the break-up of the plates considered here, as old as the middle Jurassic (*circa* 160 Mya), when the Tethys Sea divided Pangea and Laurasia and Gondwana. This is older than the earliest fossil *Kowalevskia*. If ‘Simuliini’ is older than the basal *Simulium* clade, then the origin of the family must predate the late Jurassic. Parasimuliinae and Prosimuliini (*sensu* Currie 1988) are the most basal nodes in the family (Moulton 2000), and both taxa are holarctic. A possible interpretation to that topology is that the ancestral area for the family is either the holarctic, as Currie (1988) proposed for Prosimuliini, or Pangea. Depending on the optimisation *Simulium* may have had a Pangean distribution. This distribution reinforces the idea that the family has an ancient origin, perhaps early Jurassic, which was the lowest boundary proposed by Crosskey (1990). These findings open questions about the divergence time and the geographical origin for *Simulium*, and more data, both molecular and morphological, are necessary to attempt a more refined answer.

ACKNOWLEDGEMENTS

We are grateful to Mike Sharkey (University of Kentucky, USA), Mariano Donato (Museo de la Plata, Argentina), Paula Posadas (Museo Egidio Feruglio, Argentina), Ashley Kirk-Spriggs (National Museum of Namibia, Windhoek) and two anonymous reviewers for valuable comments on the manuscript. Nelida Caligaris prepared the illustrations. This research was supported in part by the grant DIF-Ciencias-UIS 5112. The first author is indebted to *Colciencias* (Consejo Nacional de Ciencia y Técnica, Colombia) and to DIF-Ciencias-UIS for their financial support.

REFERENCES


COSCARÓN, S. 1991. Insecta, Diptera, Simuliidae, subfamilia Simuliinae, tribu Simuliini (*sensu* Currie 1988) are the most basal nodes in the family (Moulton 2000), and both taxa are holarctic. A possible interpretation to that topology is that the ancestral area for the family is either the holarctic, as Currie (1988) proposed for Prosimuliini, or Pangea. Depending on the optimisation *Simulium* may have had a Pangean distribution. This distribution reinforces the idea that the family has an ancient origin, perhaps early Jurassic, which was the lowest boundary proposed by Crosskey (1990). These findings open questions about the divergence time and the geographical origin for *Simulium*, and more data, both molecular and morphological, are necessary to attempt a more refined answer.

ACKNOWLEDGEMENTS

We are grateful to Mike Sharkey (University of Kentucky, USA), Mariano Donato (Museo de la Plata, Argentina), Paula Posadas (Museo Egidio Feruglio, Argentina), Ashley Kirk-Spriggs (National Museum of Namibia, Windhoek) and two anonymous reviewers for valuable comments on the manuscript. Nelida Caligaris prepared the illustrations. This research was supported in part by the grant DIF-Ciencias-UIS 5112. The first author is indebted to *Colciencias* (Consejo Nacional de Ciencia y Técnica, Colombia) and to DIF-Ciencias-UIS for their financial support.

REFERENCES


COSCARÓN, S. 1991. Insecta, Diptera, Simuliidae, subfamilia Simuliinae, tribu Simuliini (*sensu* Currie 1988) are the most basal nodes in the family (Moulton 2000), and both taxa are holarctic. A possible interpretation to that topology is that the ancestral area for the family is either the holarctic, as Currie (1988) proposed for Prosimuliini, or Pangea.Depending on the optimisation *Simulium* may have had a Pangean distribution. This distribution reinforces the idea that the family has an ancient origin, perhaps early Jurassic, which was the lowest boundary proposed by Crosskey (1990). These findings open questions about the divergence time and the geographical origin for *Simulium*, and more data, both molecular and morphological, are necessary to attempt a more refined answer.

ACKNOWLEDGEMENTS

We are grateful to Mike Sharkey (University of Kentucky, USA), Mariano Donato (Museo de la Plata, Argentina), Paula Posadas (Museo Egidio Feruglio, Argentina), Ashley Kirk-Spriggs (National Museum of Namibia, Windhoek) and two anonymous reviewers for valuable comments on the manuscript. Nelida Caligaris prepared the illustrations. This research was supported in part by the grant DIF-Ciencias-UIS 5112. The first author is indebted to *Colciencias* (Consejo Nacional de Ciencia y Técnica, Colombia) and to DIF-Ciencias-UIS for their financial support.

REFERENCES


COSCARÓN, S. 1991. Insecta, Diptera, Simuliidae, subfamilia Simuliinae, tribu Simuliini (*sensu* Currie 1988) are the most basal nodes in the family (Moulton 2000), and both taxa are holarctic. A possible interpretation to that topology is that the ancestral area for the family is either the holarctic, as Currie (1988) proposed for Prosimuliini, or Pangea. Depending on the optimisation *Simulium* may have had a Pangean distribution. This distribution reinforces the idea that the family has an ancient origin, perhaps early Jurassic, which was the lowest boundary proposed by Crosskey (1990). These findings open questions about the divergence time and the geographical origin for *Simulium*, and more data, both molecular and morphological, are necessary to attempt a more refined answer.

ACKNOWLEDGEMENTS

We are grateful to Mike Sharkey (University of Kentucky, USA), Mariano Donato (Museo de la Plata, Argentina), Paula Posadas (Museo Egidio Feruglio, Argentina), Ashley Kirk-Spriggs (National Museum of Namibia, Windhoek) and two anonymous reviewers for valuable comments on the manuscript. Nelida Caligaris prepared the illustrations. This research was supported in part by the grant DIF-Ciencias-UIS 5112. The first author is indebted to *Colciencias* (Consejo Nacional de Ciencia y Técnica, Colombia) and to DIF-Ciencias-UIS for their financial support.


Manuscript received November 2002; accepted April 2003.