First fossil *Molinaranea* Mello-Leitão, 1940 (Araneae: Araneidae), from middle Miocene Dominican amber, with a phylogenetic and palaeobiogeographical analysis of the genus

ERIN E. SAUPE[1]*, PAUL A. SELDEN[1,2] and DAVID PENNEY[3]

[1]*Paleontological Institute, University of Kansas, Lindley Hall, 1475 Jayhawk Boulevard, Lawrence, Kansas 66045, USA*
[2]*Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[3]*Faculty of Life Sciences, The University of Manchester, Manchester M13 9PL, UK*

The first fossil *Molinaranea* is described, from middle Miocene Dominican amber. This record extends the known range of the genus back 16 million years; it also extends the geographical range of the genus through time, with extant species known only from Chile, Argentina, the Falkland Islands, and Juan Fernandez Island. A parsimony-based phylogenetic analysis was performed, which indicates that the fossil species, ***Molinaranea mitnickii* sp. nov.**, is nested with *Molinaranea magellanica* Walckenaer, 1847 and *Molinaranea clymene* Nicolet, 1849. A modified Brooks parsimony analysis was conducted in order to examine the biogeography and origins of the fossil species in the Dominican Republic; the analysis suggests that **M. mitnickii sp. nov.** arrived in Hispaniola from South America as a result of a chance dispersal event.

INTRODUCTION

Amber from the Dominican Republic has been known to the Western world since the second voyage of Christopher Columbus to the West Indies (Sanderson & Farr, 1960), but its inclusions were not examined for at least another four centuries. Since then, extensive study of Dominican amber inclusions has provided insight into the diversity of life and palaeoecology at, and spanning, the time of amber extrusion (e.g. Perez-Gelabert, 2008). The resin was probably deposited in a single sedimentary basin during the early to middle Miocene (16–19 Mya), although the exact age is still a matter of debate (Iturralde-Vinent, 2001; see Poinar & Poinar, 1999 for an alternative view). Much of the amber comes from the northern Dominican Republic in the La Toca

Formation, a 300 m thick rock sequence characterized by siltstone and lignite lenses. Dominican amber was produced by the extinct tree *Hymenaea protera* Poinar, 1991, a member of the Fabaceae.

The first Dominican amber spider was described by Ono (1981) and placed in the family Thomisidae Sundevall, 1833. There are now around 170 fossil spider species described from Dominican amber, most of which were described by Wunderlich (1988). Wunderlich (1988) was the first to describe spiders from Dominican amber belonging to the family Araneidae Simon, 1895. The Araneidae are ecribellate, entelegyne spiders with eight eyes in two subequal rows (Jocqué & Dippenaar-Schoeman, 2007). Here we describe a new araneid species from Dominican amber. It represents the first fossil record of *Molinaranea* Mello-Leitão, 1940 and extends the known range of the genus back 16 million years. The presence of this genus in the Dominican Republic in the

*Corresponding author. E-mail: eesaupe@ku.edu

middle Miocene also extends the geographical range of *Molinaranea* through time; extant species are known only from Chile, Argentina, the Falkland Islands, and Juan Fernandez Island. A parsimony-based phylogenetic analysis was conducted on the seven extant taxa and the newly described fossil species, followed by a preliminary biogeographical analysis.

FOSSIL RECORD OF ARANEIDAE

The oldest described araneid comes from the Lower Cretaceous amber of Álava, Spain (Penney & Ortuño, 2006). Other fossil species have been described from upper Cretaceous (Turonian) New Jersey amber (Penney, 2004), the Jehol (Cretaceous) and Shanwang (Neogene) biotas of China (e.g. Zhang, Sun & Zhang, 1994; Chang, 2004, respectively), Baltic amber (mid-Eocene to early Oligocene) (e.g. Petrunkevitch, 1942), the Messel Oil Shales of Germany (lower Eocene) (Wunderlich, 1986), Florissant Insect Beds (Tertiary) (e.g. Scudder, 1890), Quesnel Tertiary Beds in Canada (Scudder, 1878), the Öhningen of Switzerland (Neogene) (Heer, 1865), and Dominican and Mexican Chiapas amber (e.g. Wunderlich, 1988). An araneid reported from early Cretaceous Lebanese amber (upper Neocomian–basal Aptian) (Wunderlich, 2004) is likely to be a misidentification according to Penney & Ortuño (2006), as is a juvenile described from Siberian amber (late Cretaceous) by Eskov & Wunderlich (1994). Orb-weavers have also been reported from Cretaceous Canadian amber (middle Campanian), but these have not been described or confirmed (McAlpine & Martin, 1969). The strictly fossil spider family Juraraneidae Eskov, 1984 described from a Jurassic non-amber fossil (which would pre-date all the above) has been suggested as being synonymous with Araneidae, although this has yet to be confirmed (Penney & Selden, 2006).

MATERIAL

The specimen was kindly donated to D. P. by Keith Luzzi, who obtained it during a visit to the La Toca region of the Dominican Republic. The amber had been cut and polished prior to being received by the authors. Further cutting and polishing was carried out in the laboratory of Dr Michael Engel (University of Kansas) in order to reveal morphological characters. Drawings were carried out under both incident and transmitted light with the aid of a camera lucida attached to a Leica MZ16 stereomicroscope. Drawings were then scanned and traced in Adobe Illustrator. Photographs were taken with a Leica DFC290 digital camera attached to a Leica M205C microscope. All measurements were taken with an ocular graticule and are in millimetres.

PRESERVATION

The specimen is preserved in a piece of clear amber measuring $14 \times 13 \times 8$ mm in size. The original piece had a small mycetophilid (fungus gnat) and mymarid wasp (Hymenoptera: Chalcidoidea: Mymaridae) (Michael Engel, pers. comm., 2008) as syninclusions that were later removed in order to observe the spider more clearly. The legs and antennae of a cockroach (order Blattaria) (Vincent Perrichot, pers. comm., 2008) also co-occur with the spider. Small pieces of unidentified organic matter are present within the amber. A band of air bubbles spans diagonally across the spider. There are no fractures within the piece. During preparation, but before the authors received the specimen, the patella and distal portion of the femur of the left, first leg were ground away. The spider appears desiccated and almost flattened, and the right, fourth leg is detached and moved to the left side of the spider (Figs 1A, 2A, C). The palps of the specimen are slightly twisted, which probably occurred when the spider was engulfed in resin. Careful observation revealed threads of silk wrapped around the spider's palps, legs, and body. Silk can also be seen emerging from the spinnerets. The tibiae of legs 1 and 2 are flattened and appear to widen distally; this is probably a result of desiccation prior to entombment in resin. Further, the macrosetae appear to arise from cuticular protrusions. Whereas extant members of *Molinaranea* possess macrosetae that arise from strong bases, the particularly prominent, tubercle-like bases in *M. mitnickii* probably result from fossilization processes. Otherwise, the specimen is extremely well preserved. The holotype (along with the detached syninclusions) is deposited in the University of Kansas Natural History Museum, Division of Entomology.

ABBREVIATIONS

Leg formula (e.g. 1423) indicates the length of each leg relative to the other legs from longest to shortest (in the example, 1 is the longest, followed by leg 4). Anatomical abbreviations: A, terminal apophysis; ALE, Anterior Lateral Eyes; AS, anterior spinneret; at, anal tubercle; bl, book lung; C, conductor; co, colulus; cx, coxa; cy, cymbium; E, embolus; en, endite; fe, femur; la, labium; ma, median apophysis; MS, median spinneret; mt, metatarsus; op, opisthosoma; pc, paracymbium; PLS, posterior lateral spinneret; ps, prosoma; pt, patella; sa, subterminal apophysis; sp, spiracle; sr, sternum; st, subtegulum; tf, thoracic furrow; ti, tibia; tr, trochanter; ts, tarsus. Institutional abbreviations: AMNH, American Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University.
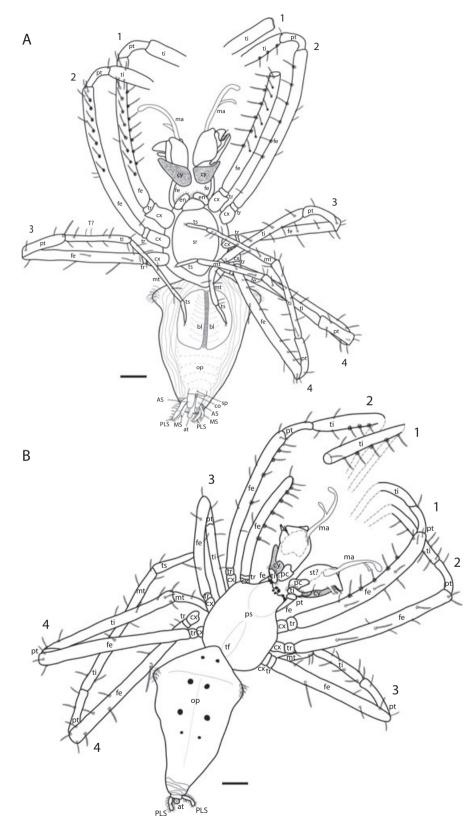
Figure 1. Interpretive drawings of ***Molinaranea mitnickii* sp. nov.**, holotype KU-NHM-ENT, DR-018. A, ventral view. Note that legs 1 and 2 are not drawn past the patella; see Fig. 2B for details. B, dorsal view. See main text for abbreviations. Scale bars = 0.5 mm.
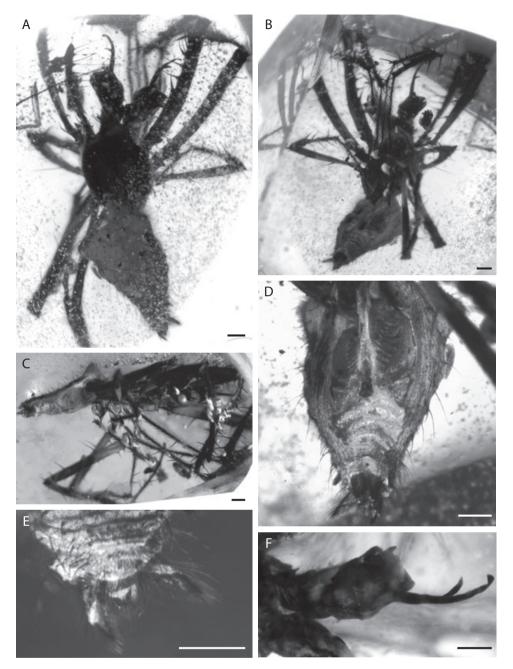
Figure 2. *Molinaranea mitnickii* **sp. nov.**, holotype KU-NHM-ENT, DR-018. A, dorsal view; B, ventral view; C, lateral view; note how the specimen appears flattened; D, ventral view of opisthosoma; the opisthosoma appears desiccated; the spiracle is visible and situated anterior to the spinnerets; the book lungs are grooved; E, view of anal tubercle and posterior lateral spinnerets; F, lateral view of left palpus; the long, bifurcating median apophysis prongs are clearly visible; although the top prong may appear longer, this is not so. Scale bars = 0.5 mm.

SYSTEMATIC PALAEONTOLOGY

ORDER ARANEAE CLERCK, 1757

ARANEIDAE SIMON, 1895

Remarks: Scharff & Coddington (1997) found four synapomorphies that support the monophyly of Araneidae. Our specimen shows three of these: the mesal orientation of the cymbium, possession of a radix, and the wide separation of lateral eye groups from the medians. The fourth, a narrow posterior median eye tapetum, is not visible in the fossil specimen. A grooved book lung cover supports the monophyly of the Araneidae apart from *Chorizopes* Pickard-Cambridge, 1870 (Scharff & Coddington, 1997), and

this character is also present in our specimen. Further, possession of a globose abdomen that overhangs the carapace, three tarsal claws, six simple spinnerets, and numerous spines on the legs are all traits commonly found in both the Araneidae and our specimen.

MOLINARANEA MELLO-LEITÃO, 1940

Type species: Molinaranea molinai Mello-Leitão, 1940
  Diagnosis: See Levi (2001).
  Distribution: Recent species are found in Chile, Argentina, the Falkland Islands, and Juan Fernandez Island. The fossil species is found in Dominican Republic amber (this paper).
  Remarks: Molinaranea was created as a monotypic genus by Mello-Leitão in 1940; the gender is feminine. Levi (2001) used the paramedian apophysis to help distinguish amongst genera of Araneidae, a structure that is unfortunately not discernable in our specimen. A filiform (thread-like) embolus is visible adjacent to the conductor, however, and distinguishes our specimen from members of *Parawixia* Pickard-Cambridge 1904 and *Ocrepeira* Marx 1883, which have robust emboli. Furthermore, our specimen can be placed with confidence within *Molinaranea* for the following reasons: the median apophysis is prominent, forked, and projects away from the palpal bulb. Although this morphology occurs in other genera, such as *Parawixia, Spilasma* Simon, 1897, and *Ocrepeira* (Levi, 1992, 1993, 1995), the details differ from those in our specimen. For example, our specimen and members of *Molinaranea* have prongs that do not re-curve as prominently as those in members of *Ocrepeira*. In those members of *Ocrepeira* that do have median apophysis prongs, the prongs are usually of unequal thickness, differing from the quasi-equal prong widths in *Molinaranea* and our specimen (Levi, 1993). Members of both *Ocrepeira* and *Parawixia* have median apophyses that typically thicken distally, whereas members of *Molinaranea* and our specimen thin distally (Levi, 1992, 1993). Members of these same genera also possess many processes, bumps and/or indentations on the median apophysis, unlike the smoother median apophyses present in *Molinaranea* and our specimen. Additionally, many *Parawixia* species with forked prongs on the median apophysis possess numerous (more than three) tubercles on the opisthosoma (more than the two present in our specimen). In *Spilasma*, the median apophysis is commonly trifid distally, with relatively short prong lengths, unlike the bi-forked prongs in *Molinaranea*. Male members of *Spilasma* also possess a ventral, sclerotized area extending from the sides of the pedicel to the genital groove (Levi, 1995), a feature lacking in our specimen.
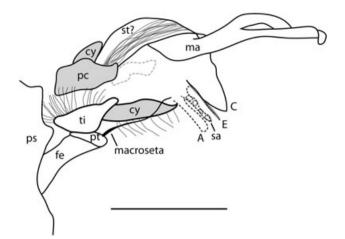

Figure 3. Interpretive drawing of the lateral view of the right palpus. The cymbium is depicted as two segments because it is splayed behind the palpal bulb (but is one cohesive structure). The bump immediately behind the median apophysis is likely the tegulum. Setae on the tibial margin are not fully illustrated. See main text for abbreviations. Scale bar = 1 mm.

MOLINARANEA MITNICKII SP. NOV. (FIGS 1–3)

Material examined: Holotype and only known specimen: Amber Fossil Collection, University of Kansas Natural History Museum KU-NHM-ENT, DR-018, adult male, Dominican amber, La Toca mines, northern Dominican Republic; coll. TerraTreasures.

Diagnosis: Molinaranea mitnickii can be distinguished from all other species by the median apophysis with long, thin/spindly, subequal prongs, resembling a lop-sided wishbone, with a proximal lobe/elbow. The ventral femora of legs 1 and 2 possess a row of strong macrosetae.

Etymology: The specific epithet is after Justin Mitnick, nephew of Keith Luzzi, the owner of TerraTreasures who found and donated the specimen for study.

Description: Body length 6.95. Carapace 2.82 long, 2.0 wide, ≥ 1.88 tall; pars cephalica only slightly elevated (approximately 0.42). Eyes small; ALE appear to be on small tubercles; numerous macrosetae in the ocular region. Details of chelicerae and fangs obscured; small. Sternum 1.41 long, 1.04 wide; relatively short and rounded; lateral margins project between coxae. Endites 0.38 long, longer than wide, suboval, tooth present. Labium 0.38, as wide as long, suboval to subcircular. Petiole attached 0.95 from anterior of opisthosoma immediately above book lungs; not sclerotized. Opisthosoma 4.13 long including spinnerets (Fig. 2D), 3.6 long without spinnerets, 2.23 at widest point, height uncertain because of flattened nature of specimen; likely to have been elongate and suboval in life; dorsal surface bears

abundant, long, scattered setae; concentrated setae on two anterior tubercles (Fig. 1B). PLS longer than MS and AS, PLS defined in two segments (Fig. 2E); AS 0.43 and PLS 0.51; colulus present, tongue-shaped with nine setae. Spiracle situated 0.03 anterior to co and 0.13 to base of AS; anal tubercle 0.34.

Leg formula 2143; leg 1 cx 0.52, tr 0.30, fe 3.16, pt 1.07, ti 4.13, mt 2.17, ts 0.63, total 11.98; leg 2 cx 0.50, tr 0.28, fe 3.44, pt 0.90, ti 4.13, mt 2.36, ts 0.64, total 12.25; leg 3 cx 0.42, tr 0.28, fe 2.36, pt 0.82, ti 1.25, mt 1.26, ts 0.48, total 6.87; leg 4 cx 0.45, tr 0.14, fe 2.43, pt 0.98, ti 2.10, mt 2.03, ts 0.46, total 8.59. Legs long; all legs possess strong macrosetae (Figs 1, 2A, B); macrosetae originate from strong cuticular bases; variable in length, longer macrosetae 0.7–0.8, shorter macrosetae 0.4–0.6; longer macrosetae appear to be concentrated on the lateral margins of tibiae 1 and 2 and ventral surfaces of most leg segments, although this is variable; row of macrosetae on prolateral to ventral margin of tibia 1 and 2; row of seven to ten macrosetae on inferior surface of femora of legs 1 and 2; row of three to four macrosetae on superior surface of femora of legs 1 and 2; femora of leg 1 with lateral row of seven to eight macrosetae; scattered macrosetae, semialigned, on ventral femora of legs 3 and 4; tibia and femur of legs 1 and 2 thicker and more robust. Hook on distal margin of the first coxa; fourth coxa with at least one macroseta. Paired tarsal claws with teeth, unpaired claw simple.

Palps large (Figs 1, 2F); length of palpal bulb without median apophysis ≥ 1.09, width 0.79; median apophysis with bifurcation into long, thin spindly prongs (Figs 2A, F, 3), resembling a wishbone; median apophysis 1.41 long; prongs on median apophysis equal, with recurved, semipointed tip; median apophysis with proximal lobe or elbow; embolus distally filiform and situated between conductor and terminal apophysis (Fig. 3); conductor broader than terminal apophysis and attached in middle of bulb with a semipointed tip; subterminal apophysis present as a narrow band between embolus and terminal apophysis (Fig. 3); terminal apophysis lobate to truncate and narrow, larger than subterminal apophysis (Fig. 3); one macroseta on patella.

Female: Unknown.

Distribution and age: Dominican Republic amber; probably middle Miocene (16–19 Mya) (see Iturralde-Vinent, 2001).

Remarks: The species can be distinguished from *Molinaranea vildav* Levi, 2001 by the presence of a proximal lobe or elbow below the radix of the median apophysis (Fig. 3) instead of above it, by the curved tip on the lower prong of the median apophysis, and by the prongs, which appear more separated (like a wishbone) in *M. mitnickii* than in *M. vildav*. Further,

M. mitnickii possesses a row of macrosetae on the ventral surfaces of femora 1 and 2, unlike in *M. vildav*. The length of the median apophysis prongs distinguishes *M. mitnickii* from *M. vildav*, *Molinaranea mammifera* Tullgren, 1902, and *Molinaranea clymene* Nicolet, 1849 (significantly shorter in *M. vildav*, *M. mammifera*, and *M. clymene*). *Molinaranea mitnickii* lacks the short, wide median apophysis characteristic of *M. mammifera* and the tufts of setae on the abdomen that are present in *M. clymene* (Levi, 2001: figs 27, 30). Unfortunately, much of Levi's description and diagnostic characters are based on colour pattern, which is usually not discernible in amber specimens.

PHYLOGENETIC ANALYSIS

TAXA ANALYSED

Molinaranea clymene Nicolet, 1849; ♂ from Chile, Osorno Prov., Puyehue, 500 m, MCZ 76602 (coll. L. E. Peña, 26.i.1969); ♀ from Chile, Osorno Prov., Termas de Puyehue, MCZ 76601 (coll. H. Levi, 10.iii.1965).

Molinaranea fernandez Levi, 2001; ♀ (holotype) & ♂ (allotype) from Chile, Juan Fernandez Isl., Mas a Tierra, Valle Anson, Plazoleto de Yunque, 200–250 m, AMNH (coll. B. Malkin, 1–28.iv.1962); ♂ & ♀ allotypes from Juan Fernandez Islands, Mas a Tierra, Valle Anson, Plazoleto de Yunque, 200–250 m, Camote Side, AMNH (coll. Borys Malkin, 1–28.iv.1962).

Molinaranea magellanica Walckenaer, 1847; ♂ from Chile, Osorno Prov., Puyehue, 500 m, MCZ 69796 (coll. L. E. Peña, 26.i.1969); ♂ from Chile, Llanquihue Prov., Correntoso, MCZ 79160 (coll. L. Peña, xii.1968); ♂ from Chile, Magallanes, Laguna Amarga, Natales, MCZ 79161 (coll. L. Peña, 14–21.xii.1960); ♂ from Chile, Llanquihue Prov., Chemisa, MCZ 79162 (coll. L. Peña, 13.xii.1968); ♀ from Chile Cautín, Villarrica, MCZ 76600 (coll. H. Levi, 3.iii.1965), and ♀ from Chile, Concepcion Prov., Rio Andalien, AMNH (coll. German Munoz, 10.iv.1977).

Molinaranea mammifera Tullgren, 1902; ♂ from Chile, Osorno Prov., 7.7 km north-east of Termas de Puyehue, Valdivian rainforest, AMNH (coll. A. Newton & M. Thayer, 19–25.xii.1982); ♂ from Chile, Osorno Prov., Parque Nac., Puyehue, 4.1 km east of Anticura, 430 m, trap site 662, AMNH (coll. A. Newton & M. Thayer, 19–26.xii.1982); ♀ from Chile, Conception Prov., Ramuntcho, MCZ 76599 (coll. Cekalovic, 22.iii.1975), and ♀ from Chile, Palena Prov., Chaiten, 0–100 m, AMNH (coll. N. I. Platnick & R. T. Schuh, 4.xii.1981).

Molinaranea phaethontis Simon, 1896; ♂ from Chile, Santiago Prov., El-Manzano, AMNH (coll. L. E. Peña, 13.x.1982); 2 ♀♀ from Chile, Region de la

Araucaría (IX), Melleco Prov., Malalcahuello, AMNH (coll. L. E. Peña, 9–15.xii.1985).

Molinaranea surculorum Simon, 1896; ♂ from Chile, region del Bío-Bío (VIII), Bío-Bío Prov., El Manzano, near Contulmo, AMNH (coll. L. E. Peña, 15.xii.1985); 2 ♂♂ & ♀ from Chile, Nuble Prov., Las Cabras, AMNH (coll. L. Umana, 26–28.xii.1986); ♂ from Chile, Valdivia, Santo Domingo, AMNH (coll. E. Krahmer, 19.ix.1976); ♂ from Chile, Region de Los Lagos (X), Valdivia Prov., Purolón, north-west of Panguipulli, AMNH (coll. L. E. Peña, 10.i.1985); ♂ from Chile, Osorno Prov. coast, Pucatrihue, MCZ 76598 (coll. L. Peña, 1.iii.1968); ♀ from Chile, Osorno Prov., Osorno Coast, MCZ 76597 (coll. L. E. Peña, i–iii.1968), and ♀ from Chile, Valdivia, AMNH (coll. E. Krahmer, 5.xii.1976).

Molinaranea vildav Levi, 2001; ♂ & ♀ from Chile, Valdivia, AMNH (coll. E. Krahmer, 8.xii.1976); ♀ (holotype) from Chile, Valdivia Prov., Valdivia, AMNH (coll. E. Krahmer, 15/20.xi.1978).

Parawixia bistriata Rengger, 1836; ♂ & ♀ from Argentina, Tucuman, MCZ 78553 (coll. J. A. Kochalka, 30.xi.1986).

Parawixia rigida Pickard-Cambridge, 1889; ♀ from Costa Rica, Heredia, La Selva, near Puerto Viejo, MCZ 81173 (coll. W. G. Eberhard, 31.i.1981); ♂ from Costa Rica, Puntarenas, Osa Peninsula, Sirena, MCZ 81174 (coll. W. G. Eberhard, 31.i.1981).

Parawixia rimosa Keyserling, 1891; ♀ from Columbia, Huila, 19.3 km east of Sta. Leticia, MCZ 80109 (coll. W. G. Eberhard, 29.ii.1976); ♂ from Columbia, San Pedro, Sierra Nevada de Santa Marta, MCZ 80978 (coll. J. Kochalka, 3.iv.1975).

N. B.: additional members of *Parawixia*, *Ocrepeira*, and *Spilasma* were also examined within the course of this study, primarily to delineate amongst palpal structures.

METHODS

The data matrix (Table 1) was analysed using PAUP v.4.0 (Swofford, 1998). Eleven species were included in this analysis. The genus *Parawixia* (Araneidae) was chosen as the outgroup, using *Parawixia bistriata* Rengger, 1836, *Parawixia rigida* Pickard-Cambridge, 1889, and *Parawixia rimosa* Keyserling, 1891 as representative members, because Levi (2001) posited that this genus is closely related to *Molinaranea*. This suggestion was based on five synapomorphies *Molinaranea* shares with *Parawixia*, *Ocrepeira*, and *Eriophora* Simon 1864, including an unusually long scape and median apophysis, the attachment of the median apophysis above the radix, the proximal sculpturing of the median apophysis at its insertion above the radix, and a projection of the median apophysis away from the palpal bulb (N. B.: both *M. clymene* and *M. magellanica* were originally misclassified as *Parawixia*). The fifth synapomorphy that Levi (2001) mentioned, distal branching of the median apophysis, is often absent in *Parawixia* (and other genera); we therefore included in our analysis two members of *Parawixia* that lack this feature, *P. bistriata* and *P. rimosa*, and one that possesses it, *P. rigida*. *Parawixia bistriata* is a common colonial orb weaver found throughout Brazil, Bolivia, Paraguay, and north-east Argentina and occupies the area between the Dominican Republic (amber fossil locality) and Chile (extant *Molinaranea* range). *Parawixia rigida* is found throughout Central America and *P. rimosa* is found in Columbia, Ecuador, Peru, and southern parts of Central America. It should be noted that Scharff & Coddington (1997) did not include *Molinaranea* and *Parawixia* in their phylogenetic analysis of the Araneidae, and therefore did not address or confirm the sister relationship of these two groups.

Table 1. Character matrix

Taxon/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
M. fernandez	1	1	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	1	1
M. magellanica	2	1	1	1	1	1	1	2	2	2	2	0	1	0&1	2	0	0	1	1
M. clymene	0	1	1	0&1	1	1	1	2	2	2	2	0	1	0&1	2	0	0	0	1
M. vildav	0	1	0	1	1	1	1	0	0	2	2	0	1	0	2	0	0	0	0
M. surculorum	1&3	0	0	0	1	1	1	1	1	2	2	0	1	0	0	0	0	0	1
M. phaethontis	1	1	1	1	0	1	0	1	1	2	2	0	1	0	1	0	0	0	1
M. mammifera	0	1	1	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1
M. mitnickii	0	1	?	1	1	1	?	2	2	1	1	0	1	?	2	0	0	?	?
P. bistriata	3	0	1	0	0	1	1	2	2	2	2	1	0	0	1	0	0	0	0
P. rigida	0	0	1	0	0	1	1	2	2	2	2	0	0	0	1	1	1	0	0
P. rimosa	3	0	1	0	0	1	1	0	2	2	2	0	0	0	1	1	1	0	0

M., Molinaranea; P., Parawixia.

An exhaustive search was performed to determine the most parsimonious tree for the data matrix. All 19 characters were treated as unordered and unweighted; multistate taxa were treated as polymorphisms. Bootstrap and jackknife analyses were conducted using 1000 replications in a heuristic, stepwise search that sampled five random trees per replication. Groups were retained that were compatible with the 50% majority rule consensus tree. A test for Bremer support was also performed (Bremer, 1988). All data were compiled into Nexus files using Mesquite v. 2.5 (Maddison & Maddison, 2008) and MacClade v. 4.08 (Maddison & Maddison, 2005). Tree graphics were created using FigTree v.1.1.2 (Rambaut, 2008) and Adobe Illustrator.

Characters: Males were the primary provider of character data because the fossil specimen is male. Female character data were used to bolster and support the positions of the extant taxa. Character 1 presents some difficulty because *P. bistriata* and *P. rimosa* do not have prongs and therefore cannot be coded for prong state. There are essentially two ways to deal with this situation: these taxa can be coded as a '?' or they can be coded as a multistate, where a particular state would indicate lack of prongs. Coding inexplicable characters as a '?' can lead to impossible ancestral states and unjustified trees and generally should be avoided (Waggoner, 1996; Lieberman, 1998). Further, coding inexplicable characters as a '?' is equivalent to ignoring data, as we know that there are no prongs present in these species (Waggoner, 1996). Therefore, we chose to code this character as a multistate, with state 3 equal to 'no prongs'. We acknowledge that in doing so this can decrease character independence and increase the weight of certain characters. We coded character 1 as a polymorphism for *Molinaranea surculorum* because we observed specimens that both lacked and possessed prongs (N. B.: if the species was coded as only possessing prongs, the topology of the tree would not change). Additionally, *M. clymene* was coded as having equal prongs in character 1, although Levi (2001) subtly hints that this species possesses a longer lower prong. Character 6 was coded as a polymorphism for *M. clymene* because Levi (2001) stated the species possesses macrosetae on the ventral side of the fourth coxae, but we did not observe this in the specimen studied. Levi (2001) noted that *Molinaranea phaethontis* Simon, 1896 lacks ventral setae on all its femora; however, rows of macrosetae were present on the third and fourth femora of the specimen that we studied. Levi (2001) also stated the ventral femora of *Molinaranea fernandez* Levi, 2001 are clothed in double rows of short macrosetae; we found only the third and fourth femora to have rows of macrosetae in this species (N. B.: both Levi and

ourselves studied male allotypes of *M. fernandez* from the AMNH). Further, Levi (1992) indicated that *P. rimosa* has a row of ventral macrosetae on the second femur, whereas we observed rows of macrosetae on all ventral femora except the first. Characters are listed below:

Male characters

1. median apophysis prongs, assuming bi-pronged – (no prongs = 3; shorter upper prong = 2; longer upper prong = 1; equal prongs = 0).
2. prongs on median apophysis – [present = 1; short or reduced (≤ ~0.08) = 0].
3. male opisthosoma shape – (hump above spinnerets = 1; lacks distinctive hump = 0). The hump was defined by the ability to draw an imaginary horizontal line from the anterior tubercles (in lateral view) of the opisthosoma to the posteriormost point of the abdomen that would intersect at a ~ 90 ° angle with a vertical line drawn from the spinnerets to the same posterior point on the opisthosoma.
4. macrosetae on ventral side of fourth coxa – (present = 1; absent = 0).
5. anterior opisthosoma tubercles – (concentrated setae present = 1; lacks concentrated setae = 0).
6. opisthosoma setae – [opisthosoma clothed in long (≥ 0.15 mm) setae, usually projecting outward from abdomen = 1; possesses short or no setae on opisthosoma = 0].
7. eye area with black/brown pigment – (present = 1; absent = 0).
8. macrosetae arrangement on ventral/ventrolateral side of first femur – [strong row present = 2; scattered or weak row (but more than three) or combination of state 2 and 0 = 1; no row of spines = 0].
9. macrosetae arrangement on ventral/ventrolateral side of second femur – [strong row present = 2; scattered or weak row (but more than three) or combination of state 2 and 0 = 1; no row of spines = 0].
10. macrosetae arrangement on ventral/ventrolateral side of third femur – [strong row present = 2; scattered or weak row (but more than three) or combination of state 2 and 0 = 1; no row of spines = 0].
11. macrosetae arrangement on ventral/ventrolateral side of fourth femur – [strong row present = 2; scattered or weak row (but more than three) or combination of state 2 and 0 = 1; no row of spines = 0].
12. strong row of macrosetae on dorsal side of fourth femur – (present = 1; absent or otherwise = 0).
13. filiform (thread-shaped) embolus – (present = 1; absent or otherwise = 0).

14. posterior macrosetae on sternum – (present = 1; absent = 0).
15. median apophysis length from base to longest prong tip – ($\geq$ 1.40 = 2; 0.84–1.18 = 1; $\leq$ 0.67 = 0). Note that these groupings are statistically significant based on a one-way unstacked ANOVA analysis with a P-value = 0.000.
16. tubercles on opisthosoma – ($\geq$ 4 present = 1; 0–3 = 1).
17. macrosetae on ventral, fourth trochanter – (present = 1; absent = 0).

Female characters
18. posterior median plate of epigynum (see Levi, 2001: fig. 6) – (plate T-shaped in ventral view = 1; Y-shaped or otherwise = 0).
19. stem of posterior median plate of epigynum – (stem of plate about as thick as the two wide lateral arms/projections = 1; no defined stem or lateral arms or stem not as thick as lateral arms = 0).

RESULTS

The parsimony analysis yielded two most parsimonious trees (Fig. 4) of 41 steps, with a consistency index of 0.6944 (excluding uninformative characters) and a retention index of 0.6944 (excluding uninformative characters). Our strongest nodes were those uniting *M. fernandez* /*M. mammifera*, *P. rigida* /*P. rimosa*, and the whole of *Molinaranea*, which had bootstrap and jackknife values (Fig. 4) of 76 & 71, 71 & 64,

and 91 & 83, respectively. The node uniting *M. fernandez* /*M. mammifera* and *P. rigida* /*P. rimosa* had a Bremer value of 1 (Bremer, 1988). We performed the test of Hillis (1991) (the g_1 statistic) to determine if our results departed from those generated using random data, which they did at the 0.01 level (g_1 value of –0.733936).

DISCUSSION

The analysis resulted in an unresolved clade that includes *M. mitnickii* (fossil taxon), *M. clymene*, and *M. magellanica*, within a larger grouping of *M. fernandez*, *M. mammifera*, and *M. vildav* (Fig. 4). *Molinaranea surculorum* was the most basal taxon. Neither the fossil taxon, *M. mitnickii*, nor what appears to be the most widespread taxon, *M. magellanica*, placed basally.

BIOGEOGRAPHICAL ANALYSIS

The genus *Molinaranea* has not been found in the fauna of the modern Dominican Republic or the surrounding areas. Although this could reflect deficient knowledge of the spider diversity in the region, it is unlikely because members of *Molinaranea* are fairly large, conspicuous spiders and weavers of orb webs. The presence of *Molinaranea* in Dominican amber (middle Miocene in age) therefore presents an interesting palaeobiogeographical question, as extant members of the genus are currently found only in the south-western portion of South America. There are
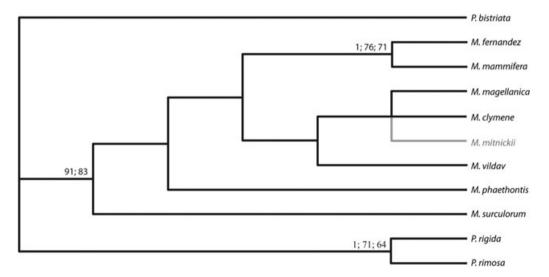

Figure 4. Strict consensus cladogram resulting from the parsimony analysis. The fossil taxon, *Molinaranea mitnickii*, is depicted in light grey; note that it does not resolve basally but rather in the middle of the tree. The nodal values are from the statistical tests: the first is the Bremer support value, the second is the bootstrap value, and the third is the jackknife value. Trees for the bootstrap and jackknife analyses were generated using 50% majority rule consensus. *M.*, *Molinaranea*; *P.*, *Parawixia*.

three general explanations for the observed pattern: (1) the genus was originally endemic to the Dominican Republic region and dispersed to South America (with subsequent divergence), later becoming extinct in the Dominican Republic and surrounding region; (2) the genus was originally endemic to South America and dispersed to the Dominican Republic where it speciated, later becoming extinct in the Dominican Republic and surrounding region; or (3) the genus was originally in South America and the Caribbean region (or was even more widespread), and divergence in the West Indies involved either vicariance or dispersal; members of the genus later became extinct throughout northern South America, the Caribbean, and any other areas. All three options must take into account the tectonic history of the region, which is a matter of contention amongst geologists (Dengo & Case, 1990; Donovan & Jackson, 1994; Hedges, 2001, 2006; Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent & Lidiak, 2006). According to Iturralde-Vinent (2006), only after the Middle Eocene was there a permanent land mass in the Caribbean that could provide a home for terrestrial biota. Donnelly (1992) and Hedges (1996c), however, although agreeing there was probably no continuous sequence of emerged land since the Cretaceous, speculated that some areas of Cuba, northern Hispaniola, and possibly Puerto Rico may have been exposed since the late Cretaceous. It should be noted that strict continent-island vicariance sensu Rosen (1975, 1985) is problematic (see Iturralde-Vinent & MacPhee, 1999 for details).

We used our strict consensus tree to perform a preliminary biogeographical study using a modified Brooks parsimony analysis (Brooks, 1985, 1990; Wiley, 1988; Lieberman & Eldredge, 1996; Lieberman, 2000) to elucidate which of the above three hypotheses might be a viable explanation for the presence of *Molinaranea* in the Dominican Republic. Although this analysis is limited by the number of fossil taxa and areas involved, it is a first step towards understanding the biogeographical patterns implied by our phylogeny.

METHODS

A detailed discussion of the methods involved in modified Brooks parsimony is beyond the scope of this paper; see Lieberman & Eldredge (1996) and Lieberman (2000) for details. We created an area cladogram by replacing the taxa with the geographical area in which the taxa were found (Fig. 5). We used six areas: (1) Dominican Republic; (2) Juan Fernandez Island; (3) south-western Chile and south-western Argentina; (4) north/central South America, including Brazil, north-east Argentina, Paraguay, and Bolivia; (5) Central America; and (6) north-west South America, including Columbia, Ecuador, and Peru. The areas were defined on both geological and biological grounds. The ancestral nodes of the area cladogram were then optimized using a modified Fitch parsimony algorithm (Fitch, 1971). The area cladogram was used to generate a geodispersal matrix, which provides insight into the relative time that barriers fell (allow-
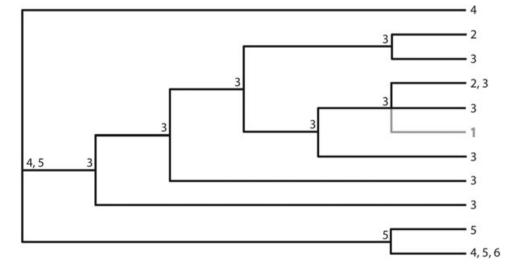

Figure 5. Area cladogram obtained by replacing terminal taxa with the areas in which they are found. These are: (1) Dominican Republic; (2) Juan Fernandez Island; (3) south-western Chile and south-western Argentina; (4) north/central South America (includes Brazil, north-east Argentina, Paraguay, and Bolivia); (5) Central America; and (6) north-west South America (includes Columbia, Ecuador, and Peru). The numbers at the nodes are the optimized locations of the ancestral taxa. The fossil taxon, *Molinaranea mitnickii*, is depicted in grey.

Figure 6. The vicariance tree and strict consensus of three geodispersal trees. The nodal numbers are bootstrap and jackknife values, respectively. Trees for the bootstrap and jackknife analyses were generated using 50% majority rule consensus; no jackknife values were obtained for the vicariance tree. A test of Hillis (1991) was also performed, and the data departed from random at the 0.01 level (g1 value of –1.572235 and –0.734178 for the vicariance and geodispersal trees, respectively).

ing for expansion of taxa), and a vicariance matrix, which provides insight into the relative time that barriers formed (isolating taxa). Each matrix was analysed in PAUP v.4.0 (Swofford, 1998) using an exhaustive search; characters were treated as ordered.

RESULTS

The vicariance analysis yielded a single most parsimonious tree of 15 steps, whereas the geodispersal analysis yielded three most parsimonious trees of 21 steps (Fig. 6). Only the Juan Fernandez Island/southwestern Chile and south-western Argentina and north/central South America/Central America nodes were resolved in both analyses. When the relationships between the vicariance and geodispersal trees are correlated, such as with Juan Fernandez Island and south-western Chile and south-western Argentina, it suggests that the processes affecting geodispersal and vicariance in these regions are similar and the regions are relatively close to each other (which they are). Coincident patterns often indicate that cyclical processes, such as rise and fall of sea level or ice sheet contraction and extension in the Pleistocene (see Extinction section below), played a role in alternating dispersal and vicariance between the two regions. The connection between north/central South America and Central America may on the one hand reflect larger-scale processes and patterns of geodispersal and vicariance, or, on the other hand, may simply be a result of sampling bias.

Results from the modified Fitch parsimony algorithm (Fig. 5) suggest that the ancestor of the Dominican fossil dispersed into the Dominican Republic from the south-western portion of South America. It must be noted that incomplete sampling as a result of extinction of taxa and lack of fossil traps in South and Central America (such as amber deposits) may have artificially biased our data by making the ancestral ranges appear more constrained than they really were. The ancestor of the Dominican fossil may have been more widespread in South America, making the mechanism of a chance dispersal event, for example from the northernmost region of South America, more realistic (i.e. the likelihood of a chance dispersal event having occurred, via any mechanism, from *southern* South America to the Caribbean is low). Unfortunately, the scarcity of fossil localities in Central and South America hinders our ability to observe what taxa were present where at different stages in the Earth's history. Members of this genus have not been found in other fossil deposits around the world, providing some indication the lineage was not globally distributed. Although our study was constrained by the limited number of fossil species and ranges and by the probable extinction that occurred within the lineage, we performed the analysis using the only data available; discovery of further fossil specimens or a modified phylogeny could verify or disprove our study. What is important is that our biogeographical analysis most strongly supports a dispersal event from South America to the Dominican Republic (rather than having originated in the Dominican Republic – option 1. A vicariant origin is similarly not supported).

DISCUSSION

Given that our data suggest a dispersal event (option 2), there are three tenable methods by which this chance dispersal could have occurred: (1) over-water dispersal *sensu* Hedges, Hass & Maxson, 1992, 1994; Hedges (1996a, b); (2) a GAARlandia (Greater Antilles + Aves Ridge) landspan around 32 Mya *sensu* MacPhee & Iturralde-Vinent (1994, 1995), Iturralde-Vinent & MacPhee (1999), and Iturralde-Vinent (2006); and (3) ballooning. Here, we discuss each of these possibilities.

1. Over-water dispersal hypothesizes that organisms arrived in the West Indies by floating on flotsam directed by ocean currents, mostly from the northeastern coast of South America (the direction of current flow). This process was thought to have occurred throughout the Cenozoic. A study by Heatwole & Levins (1972) looked at organism transport on the Puerto Rican bank and found flotsam colonized by insects, pseudoscorpions, spiders, mites, and worms 0.5–16 km out to sea. Vertebrates have also been documented to be capable of over-water travel on flotsam, especially

after seasonal hurricanes (Censky, Hodge & Dudley, 1998). There has been much dispute regarding the over-water dispersal hypothesis (see MacPhee & Iturralde-Vinent, 2005 for criticisms), and the debate continues as to whether this is a viable mechanism for the colonization of the West Indies (especially for terrestrial vertebrates).

2. The landspan hypothesis was championed by MacPhee & Iturralde-Vinent (1994, 1995) and Iturralde-Vinent & MacPhee (1999) and is based on the presumed presence of an exposed strip of land or series of islands (along the Aves ridge) running from the northern Greater Antilles to north-western South America at about the time of the Eocene–Oligocene transition. MacPhee & Iturralde-Vinent (1994, 1995) used this theory to explain the origin of vertebrates in the West Indies, but this bridge may have aided invertebrate dispersal as well. As with the over-water dispersal hypothesis, there has been heated discussion as to whether the landspan hypothesis provides a viable mechanism for the colonization of the West Indies.

3. Ballooning is the technique by which spiders extrude silken threads and are carried away on air currents. Spiders have been known to land on ships many miles out to sea (Darwin, 1839), and this dispersal ability may account for the presence of at least some spider species in the West Indies. It is important to note, however, that Miocene amber contains both highly dispersive taxa (such as the Araneidae and Tetragnathidae) and also poorly dispersive taxa (Theraphosidae and Dipluridae). Penney (2008) suggested the presence of nonballooning, poorly dispersive taxa in Miocene amber supports the GAARlandia landspan hypothesis (however, this does not refute the hypothesis that poorly dispersive taxa could have floated over on flotsam from South America *sensu* Hedges, 1996,a, b as well).

As referred to above, studies of various lineages differ on which of the dispersal and/or vicariance models is supported, and additional studies are needed in order to look for coincident patterns among different clades so as to tease apart the overall colonization pattern for the West Indies, if one is ever to emerge. Large-scale geological processes usually influence the Earth's biota in concert.

EXTINCTION

The presence of *Molinaranea* in Miocene Dominican amber and its absence from the modern fauna of Hispaniola and elsewhere in the Caribbean region suggest that the genus became extinct in the Dominican Republic, and presumably throughout much of its former range. A similar pattern can be seen in many other Dominican amber fossil arthropods. Riodinid butterflies provide a good example: two genera found in Dominican amber, *Voltinia* Stichel, 1910–11 and *Theope* Doubleday, 1847, no longer exist in the Greater Antilles, and only a single riodinid species lives there presently (Peñalver & Grimaldi, 2006). Ants offer another example: individuals of the genus *Leptomyrmex* Mayr, 1862 are present in Dominican amber, but the only members alive today reside in Australia (Poinar, 1993).

Various models have been called upon in order to explain these extinction patterns in the West Indies. Peñalver & Grimaldi (2006) have cited insularization as the cause of the riodinid extinctions in the Greater Antilles (the authors suggest that riodinid butterflies colonized the Greater Antilles when the landmasses were potentially closer to or actually fused with the mainland in the early Miocene or late Oligocene, but this is a tentative hypothesis and one that is complicated by the convoluted geology and tectonics of the region). Hall, Robbins & Harvey (2004) invoked Plio-Pleistocene cooling, habitat disruption, and xerophytization as possible extinction triggers for the riodinid butterflies and other arthropod groups, but Peñalver & Grimaldi (2006) argued that this model does not fit the riodinid example because a close living relative of the now extinct Dominican species resides in xerophytic environments in Mexico. Regardless, there seems to be a consensus that the climate in the West Indies was considerably more arid during the Pleistocene, which may have had an influence on the biota (Bonatti & Gartner, 1973; Pregill & Olson, 1981; Schubert & Medina, 1982; Schubert, 1988). The actual causes of the apparent extinctions remain unknown, and different lineages may have been influenced by different mechanisms.

The disjunct distribution between many Dominican fossil species and their extant relatives is mirrored in the rest of the world. Fossils have provided evidence (e.g. Eskov, 1987, 1992 for archaeid spiders; Wedmann & Makarkin, 2007 for mantidflies) that many lineages once thought to be Gondwanan in origin were present in the northern hemisphere and likely to be relics of a previously widespread distribution. The discovery of a fossil species of *Molinaranea* in the Dominican Republic (given modern members are restricted to southern South America) provides another example of a lineage with a likely relict extant distribution.

Modern members of *Molinaranea* inhabit three areas within the temperate rain forest of southern Chile and Argentina: the Valdivian rain forest, the north Patagonian rain forest, and the Magellanic rain forest. All of these rainforests are characterized by evergreen broadleaf trees, evergreen conifers, and

abundant epiphytes (Veblen & Alaback, 1996; Levi, 2001). As modern members of the genus reside in what appears to be a relatively constrained niche space, one might be inclined to assume that the habitat of the Dominican Republic in the middle Miocene was similar to that of southern Chile and surrounding regions. However, it is thought that Dominican amber was probably deposited in a warm, humid tropical forest, unlike the modern temperate forest of southern Chile (Iturralde-Vinent, 2001).

Pleistocene glaciations significantly affected the climate and environment of southern South America, and during glacial maxima ice would have covered most of the forest that today supports *Molinaranea* (McCulloch *et al.*, 2000; Hulton *et al.*, 2002). This suggests that members of *Molinaranea* occupied areas other than their current residence during the glaciations, perhaps tracking preferred habitat (unless they survived in mountainous refugia *sensu* Haffer, 1969 for Amazonian bird fauna). As Hispaniola was a distinct island during the Pleistocene, members of *Molinaranea* may not have been able to escape changes in climate or track habitat as effectively as their South American counterparts; this, in part, could explain their absence from the modern West Indies.

ACKNOWLEDGEMENTS

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