The endemic *Atlantochrysa atlantica* (McLachlan) (Neuroptera: Chrysopidae) on Atlantic Islands: African or American origin?

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*Atlantochrysa atlantica* (McLachlan) is restricted to Madeira and the Canary Islands. To determine its origin, molecular and morphological methods were used to identify its closest relatives among 40 species of Chrysopidae in 23 genera. Phylogenetic analysis of nuclear DNA from *PepCK*, *wg*, and *ATPase* show monotypic *Atlantochrysa* in a clade that includes American *Meleoma* and African *Cunctochrysa*; within the clade, *Atlantochrysa* is the sister taxon of those two genera together. Adult morphology and proximity to Africa suggest an origin in Africa from a *Cunctochrysa*-like ancestor, while larval morphology and habits support an origin in the Western Hemisphere from a *Meleoma*-like ancestor. A Bayesian phylogenetic analysis places the origin of this clade at around 20 mya. *Atlantochrysa* probably evolved in the early Miocene from an African relative of either *Cunctochrysa* or *Meleoma*, or from a shared African ancestor of both genera lacking the trash-carrying suite of specialisations.

**Keywords:** molecular systematics; morphology; sequence data; *Cunctochrysa*; *Meleoma*; Madeira; Canary Islands; biogeography

**Introduction**

Only seven species of Chrysopidae occur on the volcanic islands of Madeira (Portugal) and the Canary Islands (Spain) in the eastern Atlantic (Aspöck et al. 2001; Lourenco et al. 2006). Six of these species are closely related or even identical to continental taxa known from northwestern Africa or southwestern Europe. The seventh and exceptional one (Figure 1A) is the handsome species *Atlantochrysa atlantica* (McLachlan), endemic to the islands of Madeira, Tenerife, La Palma, Gran Canaria, El Hierro, and Gomera (Monserrat and Reviejo 1978). It is the largest lacewing species on these islands, and is typically associated with the moist laurophyll forests growing there.

The first specimens of *Atlantochrysa atlantica* were described by McLachlan (1882) as *Chrysopa atlantica*, based on one female from Madeira and one from the Canary Islands. McLachlan (1882) considered the new species to be most closely related to Mediterranean *Chrysopa formosa* Brauer. Tjeder (1939) separated the populations from Madeira into two new species, *Chrysopa pseudoatlantica* and *C. sororcula*, thus restricting *C. atlantica* to the populations on the Canary Islands. According to Tjeder (1939, p. 37), ‘a close relationship exists between theatlantica-group and the carnea-
group,’ implying that Atlantochrysa Hölzel might be closely related to or even derived from within the genus that we now know as Chrysoperla Steinmann.

When Hölzel (1970) created the subgenus Atlantochrysa within the huge genus Anisochrysa Nakahara, he retained the three separate, endemic Atlantochrysa species. The most detailed study of Anisochrysa (Atlantochrysa) atlantica was by Monserrat (1977), who worked principally on specimens from the island of La Palma. All larval instars and their behaviour were described in detail, as well as the distribution of the species on the Canary Islands. There was no consideration of how or where the species originated. The author stated that the species on the Canary Islands was not restricted to laurophyll forest, but occurred also on conifers and in rural parks at high elevations.

Brooks and Barnard (1990) found many insect remains in the guts of museum specimens of the three species, suggesting carnivory by the adults. Such behaviour in green lacewings is restricted almost completely to the genus Chrysopa Leach (Canard 2001). On the other hand, their analyses of male genitalia pointed to a close relationship with the genera Cunctochrysa Hölzel, Meleoma Fitch, and Plesiochrysa Adams (Brooks and Barnard 1990). In a later paper, Brooks (1997) tentatively made sister taxa of Atlantochrysa and Cunctochrysa, based on their shared possession of a ventral hook on the arcessus of the male genitalia. Also cautiously, Brooks (1997) placed those two genera into the ‘Mallada group’ with (e.g.) Mallada Navás, Pseudomallada Tsukaguchi, and Chrysoperla, whereas Meleoma and Plesiochrysa were moved to the more distantly related ‘Chrysopa group’ with (e.g.) Chrysopa, Nineta Navás, and Yumachrysa Banks. In the configurations envisioned by Brooks, however, neither the Mallada group nor the Chrysopa group has been well supported by more recent molecular studies (Winterton and de Freitas 2006; Haruyama et al. 2008). The three

Figure 1. Adult (A) and third-instar larva (B) of Atlantochrysa atlantica.
endemic island species of *Atlantochrysa* are currently synonyms under the name *A. atlantica* (Aspòck et al. 2001), rendering the genus monotypic.

When and where did this unique species originate? Where do its closest relatives live today? With molecular sequence data becoming available for an increasing number of lacewing genera, we are now in a better position to reconstruct the origin and relationships of this remarkable species.

**Materials and methods**

**Specimens**
The offspring of two gravid females from Madeira (Portugal) were used to start a lab culture. One female was collected on 7-ix-2001 at Queimadas, southwest of Santana, the other on 11-ix-2001 near Porto Moniz. The larvae were reared on *Ephestia kuehniella* (Zeller) eggs, and the adults were fed a mixture of brewer’s yeast, honey, sugar and water (Hagen and Tassan 1970). The F$_1$ adults were preserved in 96% alcohol for molecular sequencing.

Larval specimens of *Cunctochrysa* and *Meleoma* for morphological comparisons with *A. atlantica* were selected from P. Duelli’s personal alcohol collection and examined under a dissecting microscope. Specimens included various instars of *Cunctochrysa albolineata* (Killington) from Switzerland, *C. baetica* (Hölzel) from France, *C. kannemeyeri* (Esben-Petersen) from the Republic of South Africa, an undetermined species of *Cunctochrysa* from Kyrgyzstan, *Meleoma arizonensis* (Banks) and *M. furcata* (Banks) from the USA, and *M. titschacki* Navás from Nicaragua. Morphological study focused on traits known to be associated with the debris-carrying habit such as body shape, tubercle presence and size, and chaetotaxy, following the terminology and interpretations of Tauber and Tauber (2013) and Tauber et al. (2014).

**Molecular methods**
Total genomic DNA was extracted from thoracic muscle using a QuickGene DNA tissue kit S (WAKO, Tokyo, Japan). Portions of the nuclear genes *phosphoenolpyruvate carboxykinase* (*PepCK*), *wingless* (*wg*), and *sodium/potassium ATPase alpha subunit* (*ATPase*) were amplified by the same primers and PCR protocols as in a previous paper that utilised these genes (Haruyama et al. 2008). PCR products were purified by NucleoSpin® Gel and PCR Clean-up (Takara Bio Inc., Otsu, Japan) and were submitted to Greiner Bio-One Co. Ltd (Tokyo, Japan) for direct sequencing. Sequences were assembled using GENETYX-MAC v15.0 (Genetyx Corporation, Tokyo, Japan). DNA Data Bank of Japan (DDBJ) accession numbers for the three nuclear gene sequences of all specimens are shown in Table 1.

**Molecular phylogenetic analysis**
Phylogenetic trees were estimated using maximum likelihood (ML) and Bayesian inference (BI) on sequence data from *A. atlantica* plus a subset of the chrysopid species sequenced previously by Haruyama et al. (2008). Sequences were aligned by
| Taxon                             | DDBJ accession number | Collection data                                  |
|----------------------------------|-----------------------|--------------------------------------------------|
|                                 | PepCK    | wingless  | ATPase     |
| **Hemerobiidae**                 |           |           |            |
| *Micromus linearis* Hagen        | AB287526  | AB287527  | AB287528   | Japan, Chiba, 23-v-2004, N. Haruyama |
| **Nothochrysa**                  |           |           |            |
| *Kimochrysa* Tjeder sp.          | AB287888  | AB287889  | AB287890   | R.S.A., Bushmans Kloof, 5-x-2004, P. Duelli |
| *Nothochrysa fulviceps* (Stephens) | AB287529  | AB287530  | AB287531   | Switzerland, Sisseln, 3-viii-1984, P. Duelli |
| **Apochrysa**                    |           |           |            |
| *Anapochrysa voeltzkowi* (Weele) | AB287882  | AB287883  | AB287884   | R.S.A., Tsitsikama, 18-ii-2001, P. Duelli |
| *Apochrysa matsumurae* (Okamoto) | AB287532  | AB287533  | AB287534   | Japan, Chiba, 19-x-2003, N. Haruyama |
| **Chrysopinae**                  |           |           |            |
| **Ankylopterygini**              |           |           |            |
| *Ankylopteryx gracilis* Nakahara | AB287915  | AB287916  | AB287917   | Japan, Okinawa, 14-xi-2006, I. Aoki |
| *Ankylopteryx octopunctata* (Fabricius) | AB287538  | AB287539  | AB287540   | Japan, Okinawa, 19-iii-2004, N. Haruyama |
| *Semachrysa matsumurae* (Okamoto) | AB287547  | AB287548  | AB287549   | Japan, Okinawa, 19-iii-2004, N. Haruyama |
| **Belonopterygini**              |           |           |            |
| *Italochrysa italica* (Rossi)    | AB287553  | AB287554  | AB287555   | France, Le Muy, 9-viiii-1996, P. Duelli |
| *Italochrysa nigrovenosa* Kuwayama | AB287559  | AB287560  | AB287561   | Japan, Osaka, 9-vii-2005, N. Haruyama |
| **Chrysoptini**                  |           |           |            |
| *Atlantochrysa atlantica* (McLachlan) | AB820321  | AB820322  | AB820323   | Madeira, Porto Moniz, 11-ix-2001, P. Duelli |
| *Bornochrysa squamosa* (Tjeder)  | AB287885  | AB287886  | AB287887   | R.S.A., Drakensberg, Clarens 6-ii-2002, P. Duelli |
| *Brinckochrysa kintoki* (Okamoto) | AB287574  | AB287575  | AB287576   | Japan, Chiba, 20-ix-2004, N. Haruyama |
| *Brinckochrysa turkanensis* (Navás) | AB287580  | AB287581  | AB287582   | R.S.A., WCP, Cederberg, 2-xxii-2004, P. Duelli |
| *Chrysemosa jeanneli* (Navás)    | AB287583  | AB287584  | AB287585   | R.S.A., WCP, Cederberg, 22-ii-2001, P. Duelli |
| *Chrysoptera dorsalis* Burmeister | AB287589  | AB287590  | AB287591   | Spain, Ondarroua, 17-vii-2006, P. Duelli |
| *Chrysoptera viridana* Schneider | AB287631  | AB287632  | AB287633   | Italy, Ferrara, 21-vi-2005, P. Duelli |
| *Chrysoptera carnea* (Stephens)  | AB287643  | AB287644  | AB287645   | Germany, Commercial strain |
| *Chrysoptera comans* (Tjeder)    | AB287903  | AB287904  | AB287905   | R.S.A., Drakensberg, Clarens, 15-ii-2002, P. Duelli |
| Species                                | Accession Numbers | Location                       | Collector         |
|----------------------------------------|-------------------|--------------------------------|-------------------|
| Chrysoperla furcifera (Okamoto)        | AB287652 AB287653 AB287654 | Japan, Chiba, 9-ix-2003 | N. Haruyama       |
| Chrysoperla pudica (Navás)             | AB287673 AB287674 AB287675 | R.S.A., Cederberg, 2-x-2004 | P. Duelli         |
| Chrysotropia ciliata (Wesmael)         | AB287685 AB287686 AB287687 | Japan, Yamanashi, 7-viii-2004 | A. Mochizuki     |
| Cunctochrysa albolineata (Killington)  | AB287700 AB287701 AB287702 | France, Lourdes, 19-vi-2006 | P. Duelli         |
| Cunctochrysa kannemeyeri (Esben-Petersen) | AB287891 AB287892 AB287893 | R.S.A., WCP, Wolfdrift, 1-x-2004 | P. Duelli       |
| Cunctochrysa baetica (Hölzel)          | AB820324 AB820325 AB820326 | France, Carcès VAR, 23-vii-2004 | P. Duelli       |
| Pseudomallada alcestes (Banks)         | AB287709 AB287710 AB287711 | Japan, Okinawa, 17-iii-2004 | N. Haruyama       |
| Pseudomallada flavifrons (Brauer)      | AB287736 AB287737 AB287738 | Italy, Ferrara, 21-vi-2005 | P. Duelli         |
| Pseudomallada formosanus (Matsumura)   | AB287739 AB287740 AB287741 | Japan, Chiba, 11-ix-2003 | N. Haruyama       |
| Pseudomallada prasinus (Burmeister)    | AB287778 AB287779 AB287780 | Switzerland, Leuk, 3-v-2006 | P. Duelli         |
| Mallada basalis (Walker)               | AB287808 AB287809 AB287810 | Taiwan, cultured strain  |                  |
| Mallada desjardinsi (Navás)            | AB287811 AB287812 AB287813 | Japan, Chiba, 10-ixi-2003 | N. Haruyama       |
| Mallada krakatauensis (Tsukaguchi)     | AB287826 AB287827 AB287828 | Japan, Hokkaido, 19-ixi-2005 | N. Haruyama       |
| Meleoma arizonensis (Banks)            | AB287832 AB294231 AB287833 | USA, Arizona, 7-vii-2003 | P. Duelli         |
| Meleoma furcata (Banks)                | AB287834 AB287835 AB287836 | USA, Arizona, 5-vii-2003 | P. Duelli         |
| Nineta itoi Tsukaguchi                 | AB287846 AB287847 AB287848 | Japan, Yamanashi, 7-vii-2004 | A. Mochizuki     |
| Nineta pallida (Schneider)             | AB287852 AB287853 AB287854 | Switzerland, Zürich, 19-vii-2006 | P. Duelli   |
| Peyerimhoffina gracilis (Schneider)    | AB287867 AB287868 AB287869 | Switzerland, Zürich, 27-vii-2006 | P. Duelli  |
| Plesiochrysa lacciperda (Kimmins)      | AB287870 AB287871 AB287872 | India, cultured strain |                  |
| Plesiochrysa ramhuri (Schneider)       | AB294225 AB294226 AB294227 | Australia, Chichester, 8-xi-2000 | P. Duelli    |
| Suarius walsinghami Navás              | AB287873 AB287874 AB287875 | Spain, Alhaurin de la Torre, 2-ix-2001 | P. Duelli |
| Yumachrysa apache (Banks)              | AB287876 AB287877 AB287878 | USA, New Mexico, 13-vii-2003 | P. Duelli       |

Note: PepCK: phosphoenolpyruvate carboxykinase; ATPase: sodium/potassium ATPase alpha subunit.
The total sequence length of the alignment was 1419 bp, comprising 483 bp of PepCK, 528 bp of wingless, and 408 bp of ATPase. Micromus linearis Hagen (Hemerobiidae) served as the outgroup. Forty species from 23 genera of Chrysopidae were included (Table 1).

ML analyses were performed using MEGA v5.2.2 (Tamura et al. 2011). These were applied to each gene independently and then to the three genes combined. For each of the four analyses, we used the best nucleotide substitution model as determined by MEGA (Table 2). All ML trees were generated using 1000 bootstrap replicates to evaluate statistical confidence at each branch (Felsenstein 1985).

MRBAYES v3.2.1 (Ronquist et al. 2012) was used for dedicated Bayesian (BI) phylogenetic analysis of the data, while BEAUTI and BEAST v1.8.0 (Drummond et al. 2012) added the capability of estimating dates of branching points in a Bayesian framework. In MRBAYES, the alignment for the combined data was partitioned by codon position for each gene and a separate partition-specific substitution model was determined using the greedy algorithm in PARTITIONFINDER v1.1 (Lanfear et al. 2012). The best partitioning scheme and substitution models are shown in Table 3. The Markov chain Monte Carlo analysis (MCMC) ran for 1.5 million generations. The Average Standard Deviation of Split Frequencies (ASDSF) was 0.007 at the end of the analysis. Trees were sampled every 100 generations, discarding the first 25% of trees as burn-in. In the BEAST analysis, data were partitioned by gene (but not codon position) and run under the GTR + I + Γ base substitution model applied to each partition independently. To estimate the dates of node divergence, ‘Trees’ were set to ‘Speciation: Yule Process’ and the clock was specified as ‘Lognormal Relaxed (Uncorrelated)’ with ‘Estimate’ enabled. The clock was calibrated using a fossil-

| Data set | Best model |
|----------|------------|
| Combined data (1419 bp) | TN93 + I + Γ |
| PepCK (483 bp) | TN93 + Γ |
| wingless (528 bp) | TN93 + I + Γ |
| ATPase (408 bp) | TN93 + I + Γ |

| Subset | Subset partitions (nuclear genes and codon positions) | Best model |
|--------|------------------------------------------------------|------------|
| 1      | PepCK pos.1, wg pos.1, wg pos.2, ATPase pos.1       | GTR + I + Γ |
| 2      | PepCK position2                                      | JC + Γ     |
| 3      | PepCK pos.3, wg pos.3, ATPase pos.3                 | TVM + I + Γ |
| 4      | ATPase position2                                     | K81 + I    |
based prior of 180 ± 8 million years for the age of the most recent common ancestor of Hemerobiidae and Chrysopidae (Ren and Guo 1996; Winterton et al. 2010). The MCMC was run for 10 million generations, discarding the first 10% of runs. We confirmed with TRACER v1.6 (Rambaud and Drummond 2013) that all likelihoods converged (i.e., Estimated Sample Size (ESS) of the posteriors = 364, ESS of the likelihoods = 1756). Trees were sampled every 2500 generations, discarding the first 10% as burn-in. In both types of BI analysis, posterior probabilities (PP) were calculated to evaluate statistical confidence at each node.

Results

Molecular phylogenetics

Among the 18 other chrysopine genera and in all phylogenetic analyses, Atlantochrysa atlantica clustered most closely with Cunctochrysa (Africa and Eurasia) and Meleoma (Americas). In the combined Bayesian, combined ML, and individual PepCK ML analyses, it was inferred to be the sister taxon of the clade Cunctochrysa + Meleoma (PP = 1.00, ML bootstrap values = 84% for combined data and 61% for PepCK alone). In all trees of partial or combined data the six species in the three genera formed a strongly supported clade (Bayesian PP = 1.00, ML bootstrap values = 100% for combined data, 98% for PepCK, 91% for wg, and 76% for ATPase). All trees generated under both inference methodologies and for either partial or combined data showed generally consistent topologies (see Supplemental Material). Divergence of Atlantochrysa from Cunctochrysa + Meleoma was estimated by BEAST to have occurred 19.5 ± 5.8 mya, giving a range of origination, within the 95% highest posterior density (HPD) interval, of 9.8–31.1 mya (Figure 2).

Adult morphology and behaviour

The general colour of A. atlantica was dark, mossy green, cryptically adapted for living in the moist evergreen laurophyll forests where it is most often found (Figure 1A). The only lacewing species in our study that resembled it was C. kannemeyeri from South Africa. Another endemic island genus, some of whose members are dark green and resemble Atlantochrysa closely, is Hawaiian Anomalochrysa McLachlan. Anatomically, however, Brooks and Barnard (1990) and Brooks (1997) placed Anomalochrysa close to Mallada Navás, and Mallada definitely did not cluster phylogenetically with Atlantochrysa in our analyses (Figure 2). Unfortunately, Anomalochrysa could not be included in this study.

We were not able to induce the lab-reared adults of A. atlantica to emit the foul-smelling allomones that are characteristic of the other genera in this clade: all Meleoma and Cunctochrysa species stink when stressed. It was possible, however, that field-collected Atlantochrysa specimens did stink, but not enough for us to have noticed, or that the smell was less intense or absent in lab-reared individuals. None of the papers on Atlantochrysa, including the detailed study by Monserrat (1977), mention any foul odours.

Brooks and Barnard (1990) noted many insect remains in the guts of museum specimens of A. atlantica, which could indicate a taxonomic relationship with the predatory genus Chrysopa. We reared several generations of A. atlantica on a yeast
mixture without any insect food. Offering aphids (*Acyrtosiphon pisum* (Harris)) did not result in predation. Quite clearly, living prey was not a prerequisite for oviposition in *A. atlantica*. Possibly the insect remains found in the museum specimens (Brooks and Barnard 1990) were not prey taken up intentionally, but were insect fragments sticking to the honeydew of auchenorrhynchan and sternorrhynchan insects. Scraping or licking honeydew from leaves and twigs is typical for many Neuroptera, particularly for non-predacious chrysopid adults (Principi and Canard 1984).

**Eggs**

Monserrat (1977) described and illustrated a strange pattern of disorganised egg deposition, where egg pedicels were placed on top of eggs already on pedicels. We never observed such behaviour and assume that this was an artifact of rearing adults in close confinement. However, the egg stalks were indeed very flimsy and could hardly hold up the egg. A similar type of weak egg pedicel has been noted in the endemic Hawaiian island species *Anomalochrysa frater* Perkins (Duelli 1984), where it was interpreted as an evolutionary step towards losing the egg pedicel on isolated islands lacking strong egg predation.

**Larvae**

Monserrat (1977) mentioned the agile first instar, and indeed, they are by far the fastest young lacewing larvae we have ever encountered (Duelli, unpublished). They ran on relatively long legs with sudden stops, similar to formicine ants. The only other lacewing genus with very fast young larvae is *Brinckochrysa* Tjeder (Duelli and Mochizuki, unpublished), but in that case the larvae move on short legs, more like hemerobiid larvae.

Monserrat (1977) described all larval stages and found no sign of trash-carrying behaviour. We also found no trash-carrying larval stadia in the Madeiran sample (Table 4).

Chrysopid larvae tend to be conservative in the expression of morphological features within higher taxonomic levels. Whereas adults might differ markedly

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**Figure 2.** Bayesian inference (BI) molecular phylogenetic tree generated by BEAST v1.8.0 for 40 species of Chrysopidae, including *Atlantochrysa atlantica*. The tree is inferred from a combined analysis of three nuclear genes; it is superimposed on a geological time scale estimated within a Bayesian framework using a molecular clock calibrated from the fossil record (see text). The total sequence length of the alignment was 1419 bp, comprising 483 bp of *PepCK*, 528 bp of *wg*, and 408 bp of *ATPase*. Values placed to the left of each node are Bayesian PPs ≥ 0.80/ML bootstrap values ≥ 50%; values to the right of each node are estimated dates of most recent common ancestors (MRCA). Dashes (-) mark branches with less than 0.80 PP or less than 50% bootstrap support. For the ‘*Mallada* clade’, ‘*Atlantochrysa* clade’, and ‘*Chrysopa* clade’, the mean estimated date of the MRCA is shown within a shaded horizontal bar spanning the range of upper and lower estimates calculated for 95% HPDs (see text). Members of the *Atlantochrysa* clade are highlighted using coloured fonts. The long branch to the outgroup, *Micromus linearis* (Hemerobiidae), is excluded for clarity.
between species, the larvae within a genus are often very similar to one another (Díaz-Aranda and Monserrat 1995; Díaz-Aranda et al. 2001; Henry et al. 2002; Tauber and Tauber 2013). We compared the larval morphology of the closely related genera Atlantochrysa (one species), Cunctochrysa (four species), and Meleoma (three species) to look for additional phylogenetic clues (Table 4; see Methods for the specific taxa examined). The larval head markings of both Cunctochrysa and Meleoma were very similar to those of A. atlantica (Figure 1B). All three Cunctochrysa species examined had a humped or globose body shape; relatively long, densely packed, broadly hooked setae on prominent cylindrical thoracic lateral tubercles; and dorsal abdominal setae that were similarly long, dense, and hooked or knobbed. Meleoma larvae had fusiform but somewhat hump-backed bodies; shorter and usually hemispherical thoracic lateral tubercles clothed with shorter, straight (not hooked or knobbled) setae; and fewer straight, short hairs on the abdominal dorsum. Meleoma larvae were judged more similar than Cunctochrysa to A. atlantica larvae, which exhibited a flat, fusiform body shape; low, hemispherical thoracic lateral tubercles; and short,
straight, sparse setae on the dorsal surfaces of both thorax and abdomen (Table 4; Figure 1B).

Discussion
According to our molecular sequence data (Figure 2 and Supplemental Material), the closest likely relatives of Atlantochrysa among the taxa in the analyses are the genera Cunctochrysa and Meleoma, with which Atlantochrysa forms a robust monophyletic clade. Unfortunately, variable placement of Meleoma and Cunctochrysa relative to each other in those trees renders one or both genera paraphyletic or polyphyletic, so we cannot assign Atlantochrysa an exact position relative to either genus. Nonetheless, it seems plausible that Atlantochrysa shared a common ancestor with some now-extinct taxon assignable to either Cunctochrysa or Meleoma.

Atlantochrysa larvae are not debris carriers, whereas Cunctochrysa larvae carry detritus. Accordingly, larval morphology (fusiform body shape, low tubercles, and no long setae or hooked thoracic and abdominal hairs for securing the trash packet) suggests a closer relationship of Atlantochrysa to naked Meleoma than to trash-carrying Cunctochrysa (Table 4). However, Meleoma is restricted to the Americas. To reach Madeira or the Canary Islands, an American Meleoma-like ancestor would have to disperse at least 3600 km over the Atlantic Ocean – without also becoming established in nearby Africa or Europe. This is an improbable hypothesis [although note that the damselfly Ischnura hastata (Say) is known to have colonised the Azores Islands from North America; see Cordero Rivera et al. (2005 #27473)]. A more likely ancestor is a Cunctochrysa-like species, perhaps similar to C. kannemeyeri in South Africa. Cunctochrysa is widespread in Europe, Asia and Africa, and the tiny C. baetica even today lives in patches of evergreen forest in the Atlas Mountains of northern Africa (Aspöck et al. 2001). Moreover, the morphological findings of Brooks and Barnard (1990) and Brooks (1997) place Atlantochrysa and Cunctochrysa together as closest relatives. Thus it is more compelling to postulate that Atlantochrysa shared a most recent common ancestor with some now-extinct African Cunctochrysa species, or alternatively with an extinct common ancestor of Cunctochrysa and Meleoma, also in Africa, that lacked the trash-carrying suite of specialisations.

The Atlantic island of Madeira and the Canary Islands have been continuously and sequentially formed by volcanic activity over geological ‘hot spots’, beginning nearly 60 mya (Kim et al. 2008; Fernández-Palacios et al. 2011). There was never any bridge to the mainland. Whereas Madeira is 600 km away from western Africa, minimum distances from the mainland to the Canary Islands are only about 200 km. All insect species had to get there on the wing, or they were transported on floating objects or by humans. Most lacewing species on these Atlantic islands have close relatives on the mainland in western Africa, so their origin is more or less obvious. This is not true for A. atlantica. Today, no known likely ancestor lives in western Africa. We have to keep in mind, however, that the westernmost parts of Africa, from the Atlas Mountains to Senegal, were not nearly as dry in the Miocene and Pliocene Epochs as they are today (Kutzbach and Liu 1997; Fernández-Palacios et al. 2011). Based on our estimated origination date centred on 20 mya, the first colonising population of ancestral A. atlantica reached the islands in a wetter period, when extensive evergreen forests grew in the northwestern part of Africa.
(Fernández-Palacios et al. 2011). *Atlantochrysa atlantica* does not occur on the Atlantic islands of Cape Verde, 1600 km south of the Canary Islands (Hölzel and Ohm 1990). Consequently, direct immigration from tropical Africa seems unlikely.

Numerous other island endemics on Macaronesia are also thought to have colonised the archipelagos from western Africa and to have then undergone modest adaptive radiations there, perhaps populating new volcanic islands to the west as those appeared over time. For example, mitochondrial molecular divergence of the butterfly genus *Gonepteryx* (Pieridae), coupled with the known geological history of the Canary Islands and Madeira, strongly implicate dispersal of a most recent common ancestor from Africa to Gomera, followed later by sequential dispersal from Gomera to Tenerife and from Tenerife to La Palma (Brunton and Hurst 1998). An older endemic species of *Gonepteryx* on Madeira is considered to represent a separate colonisation event from Africa. Another study of 18 species of *Nephroma* Acharius lichens, using DNA sequences from three loci, found evidence of neoendemism on the Canary Islands and Madeira, dating back to independent colonisation events 14 and 26 mya (Sérusiaux et al. 2011). A similar strategy of dispersal and evolution is seen in several plant lineages now found on Madeira, which are inferred from cpDNA and nuclear ITS sequence data to have populated that island from founders generated in an earlier adaptive radiation on the Canary Islands (Kim et al. 2008). In all three examples just described, earliest colonisation events are estimated to have occurred between three and 30 mya, which is compatible with our own broad estimate – between 10 and 30 my – for the divergence of *Atlantochrysa* from its most recent common ancestor with *Cunctochrysa + Meleoma*. However, we cannot say for sure whether dispersal of proto-*Atlantochrysa* to the archipelagos was from Africa to the Canary Islands and then Madeira, or to each island group more or less simultaneously via independent colonisation events. Nor do we know whether *Atlantochrysa atlantica* acquired its unique traits on the mainland, or only after dispersal to the islands. In any case, sufficient time has elapsed since then to erase any definitive morphological, ecological, or behavioural evidence that could have been used to clarify *Atlantochrysa’s* phylogenetic position relative to *Meleoma* or *Cunctochrysa*.

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**Supplemental material**

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