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To cite this article: Fernando H. A. Farache, Jean-Yves Rasplus, Dany Azar, Rodrigo A. S. Pereira & Stephen G. Compton (2016) First record of a non-pollinating fig wasp (Hymenoptera: Sycophaginae) from Dominican amber, with estimation of the size of its host figs, Journal of Natural History, 50:35-36, 2237-2247, DOI: [10.1080/00222933.2016.1193646](https://doi.org/10.1080/00222933.2016.1193646)

To link to this article: <http://dx.doi.org/10.1080/00222933.2016.1193646>

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First record of a non-pollinating fig wasp (Hymenoptera: Sycophaginae) from Dominican amber, with estimation of the size of its host figs

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ABSTRACT

Fig trees and their pollinating fig wasps arose about 75 million years ago in the Cretaceous period. Several other groups of chalcid wasps also utilize figs for larval development, including sycophagines, the putative sister group to pollinating fig wasps. Whereas stone and amber fossil pollinators are known, no fossils representing non-pollinating fig wasp groups have been confirmed previously. Here, we describe the first Sycophaginae from the c.15–20 Ma Dominican amber, *Idarnes thanatos* sp. nov. Farache, Rasplus, Pereira and Compton, and discuss its relationships within the *Idarnes carne* species group. Additionally, we use linear regression to compare body size, ovipositor sheaths length, and host fig size data from extant *Idarnes* species to estimate the size of its host figs. *Idarnes thanatos* was most likely associated with small to medium sized figs (diameter ≤ 1.0 cm), that were likely to have been dispersed by birds and primates. The discovery of this close relative of extant non-pollinating fig wasps suggests that early Miocene and modern fig wasp communities may share similar ecological and functional features.

ARTICLE HISTORY

Received 1 October 2015
Accepted 20 May 2016
Online 12 July 2016

KEYWORDS

Agaonidae; Chalcidoidea; *Ficus*; fossil insect communities; Miocene; palaeoecology

Introduction

The association between fig trees (Moraceae, *Ficus*) and their pollinating fig wasps (Chalcidoidea, Agaonidae, Agaoninae) is one of the most well-known examples of plant–insect mutualism (Cook and Rasplus 2003; Kjellberg et al. 2005). Fig trees and their pollinating wasps probably arose about 75 million years ago in the Cretaceous period (Cruaud et al. 2012) and subsequently diversified to generate the 750+ fig tree species and more than 1000 pollinator species present today (Berg and Corner 2005).

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<http://zoobank.org/urn:lsid:zoobank.org:pub:487327C0-129D-4696-864A-D87CA6DA243E>

 Supplemental data for this article can be accessed here.

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Figs (syconia) are enclosed hollow inflorescences lined with many tiny flowers. Adult female pollinator fig wasps enter receptive figs through a small apical pore, called the ostiole, in order to lay their eggs inside some of the female flowers (Galil and Eisikowitch 1968). They show several morphological adaptations that allow them to enter the figs, carry pollen, and pollinate, including a modified head, antennae and mandibular appendages, and those species that actively pollinate also have pollen pockets and coxal combs (Ramírez 1974, 1978; Cook and Rasplus 2003).

Apart from pollinating fig wasps, several other lineages of Chalcidoidea utilize figs as oviposition sites, but only a very few species pollinate the fig flowers and so their relationship with *Ficus* is antagonistic rather than mutualistic. These lineages are known as non-pollinating fig wasps (NPFW). Most species have long exerted or coiled ovipositors that allow them to lay their eggs from the outside of the figs, but some NPFW enter the figs to lay their eggs. According to the latest phylogenetic analyses (Heraty et al. 2013), most of the NPFW subfamilies that were at one time placed in Agaonidae are now assigned to Pteromalidae, while the Sycophaginae are recognized as one subfamily of Agaonidae, together with the pollinating fig wasps.

Among the six subgenera of *Ficus*, the Sycophaginae NPFWs are strictly associated with *Ficus* subgenera *Sycomorus* and *Urostigma*. Molecular clock analyses suggest that Sycophaginae may have originated in the Palaeocene (50–40 Ma), after the break-up of Gondwana (Cruaud et al. 2011a), but they have subsequently achieved a pantropical distribution. There are only about 60 species of Sycophaginae described to date, but the real diversity of the group is hard to estimate due to the high number of undescribed species found in recent studies (Cruaud et al. 2011b; Farache et al. 2013; Farache and Rasplus 2014).

Within Sycophaginae, *Idarnes* is the second most speciose genus, with 23 species described from the Americas, and forms the most conspicuous group of NPFWs in the Neotropical region (Gordh 1975; Bouček 1993; West and Herre 1994). *Idarnes* is associated with *Ficus* subgenus *Urostigma*, section *Americana* and is divided into three monophyletic (Cruaud et al. 2011a, 2011b) and morphologically recognizable (Bouček 1993) species-groups, namely the *I. carme*, *I. flavicollis* and *I. incertus* sp. gps. In addition to their morphological divergence, these species groups show different life history strategies and larval feeding habits (Cruaud et al. 2011b; Elias et al. 2012).

Species belonging to the *I. incertus* sp. gp are larger than co-occurring pollinator fig wasps and have relatively shorter ovipositors. They arrive early during fig development and probably induce galls in the fig receptacles (Bronstein 1999). Species belonging to the *I. flavicollis* sp. gp are about the same size or slightly larger than pollinators and their ovipositors are longer than those of pollinators and other co-occurring species. They arrive at the same time as pollinators, induce galls in fig pistillate flowers, and probably compete with pollinators for oviposition sites (Elias et al. 2012). Members of the *I. carme* sp. gp are about the same size as pollinators with relatively longer ovipositors (but usually shorter than in the *I. flavicollis* sp. gp). They arrive after pollination and are probably cleptoparasites that kill pollinators (Elias et al. 2012).

Within non-sycophagine Agaonidae, three fossil pollinator species have been described from Dominican amber (Mid Miocene) (Peñalver et al. 2006): *Tetrapus apopnus* Peñalver and Engel, 2006; *Tetrapus delclosi* Peñalver and Engel, 2006; and *Pegoscapus peritus* Peñalver and Engel, 2006, but additional undescribed species are known. *Archaeagaon*

minutum (Donisthorpe, 1920) was collected from the Isle of Wight Insect Limestone (Late Eocene) and although originally described as an ant (*Ponera*), is clearly a pollinating fig wasp (Compton et al. 2010; Antropov et al. 2014). Much less evidence of fossil NPFW is available. *Parviformosus wohlraabeae* Barling, Heads and Martill, 2013 was described from the lower Cretaceous of Brazil and was considered as a possible sycophagine, based in part on its long ovipositor (Barling et al. 2013). However, *P. wohlraabeae* lacks the apomorphic characters that could place it in Chalcidoidea and whether it is truly a fig wasp remains to be demonstrated. No other putative fossil NPFW have been described.

In this paper we describe the first confirmed fossil NPFW as *Idarnes thanatos* sp. nov. based on a single female from Dominican amber. Based on its morphology and comparisons with extant *Idarnes* and *Ficus* species we also estimate the size of the figs where it laid its eggs, from which we infer the plant's likely seed dispersal agents.

Materials and methods

Dominican amber and specimen preparation

The Dominican amber has been dated as Mid-Miocene (15–20 million years ago) and its resin is probably derived from a single extinct *Hymenaea* (Papilionaceae) species (Iturralde-Vinent and MacPhee 1996). The specimen was acquired from a commercial source by S. G. Compton and prepared at Muséum National d'Histoire Naturelle in Paris, by D. Azar. According to the suppliers, the specimen was excavated in the La Bucara amber mines in 2008. The amber piece included the described specimen, one large leaf/leaflet, an ant specimen (Formicidae) and another chalcid wasp (Supplementary File 1).

Protocols for imaging and description mostly followed Farache and Rasplus (2014). Morphological terminology follows Gibson (1997) and the HAO portal (Yoder et al. 2010). The specimen was photographed using a Leica M16 zoom lens attached to a JVC KY-75U 3CCD digital camera and a portable computer workstation running EntoVision Imaging Suite software (GT Vision, Hagerstown, MD USA). Cartograph 5.6.0 (Microvision, Evry, France) software was subsequently used to merge the image series. Illumination was achieved using a 'quadrant' setup, with four fibre optic light guides stemming from two individual light sources (Leica CLS 150 X), similar to the method described by Buffington and Gates (2008).

Abbreviations and acronyms

Abbreviations for measurements include: *L* = length; *W* = width; *H* = height; *F_x* = funicular segment *x*, *FD* = fig diameter, *BL* = body length, *OL* = ovipositor sheaths length, and *OB* = ratio of ovipositor sheaths/body length.

Acronyms for specimen depositories and their respective curators include: MZSP, Brazil, São Paulo, São Paulo, Museu de Zoologia da Universidade de São Paulo (Carlos Roberto Ferreira Brandão); CDBGP, France, Montferrier-sur-Lez. Centre de Biologie pour la Gestion des Populations (Emmanuelle Artige).

Estimation of host fig size

We recorded body length (BL), ovipositor sheaths length (OL), and the ratio of ovipositor sheaths/body length (OB) for 11 described *Idarnes* species and 20 undescribed species. Since differences in life histories in Sycophaginae are related to morphological characters such as body size and ovipositor length (Cruaud et al. 2011b) we restricted the analysis to species that were in the species group to which *I. thanatos* can be assigned (*Idarnes carme* sp. gp *sensu* Bouček (1993), as explained below). The specimens analysed are deposited in the Jean-Yves Rasplus collection at CBGP (France) and the Rodrigo A. S. Pereira collection at USP Ribeirão Preto (Brazil.) Body measurements were taken from 31 wasp species, with a total of 136 specimens measured. Measurements were mostly taken from three to six specimens per species. When fewer or no specimens were available, we measured all available specimens or took the information from the literature (Gordh 1975; see Supplementary File 2 for further information on specimen sampling). The fig wasps were photographed using a Leica MZ16 (Leica Microsystems, Heerbrugg, Switzerland) stereomicroscope and measured with ImageJ software (Abràmoff et al. 2004) and Leica application suite V3.6.

Fig diameters (FD) for each species were taken from the literature (Burger 1977; Berg and Villavicencio 2004; Berg 2009). These references cited the maximum and minimum fig diameter, and therefore we took the median of these values (excluding outlier values when they were present in the descriptions). Measurements of wasps and figs are recorded in Supplementary File 2.

We performed linear regressions using the following models: BL~FD, OL~FD, and OB~FD. These regressions were performed using both maximum and median fig sizes as predictors. In order to select the best-fitting model, we compared the R^2 regression index among the models and used the best-fitting model to predict the 95% confidence interval (CI) of fig diameter using the characteristics of the fossil specimen. The graphic regression diagnostics, quantile–quantile plots, and distribution of residuals for the estimated models confirmed that there was no violation of linear model assumptions. All analyses were performed using the R statistical environment (R Core Team 2015).

Results

Systematic palaeontology

Order **HYMENOPTERA** Linnaeus, 1758

Suborder **APOCRITA** Gerstaecker, 1867

Superfamily **CHALCIDOIDEA** Latreille, 1817

Family **AGAONIDAE** Walker, 1846

Subfamily **SYCOPHAGINAE** Walker, 1875

Idarnes Walker, 1843

Idarnes thanatos Farache, Rasplus, Pereira and Compton, sp. nov.

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Figure 1

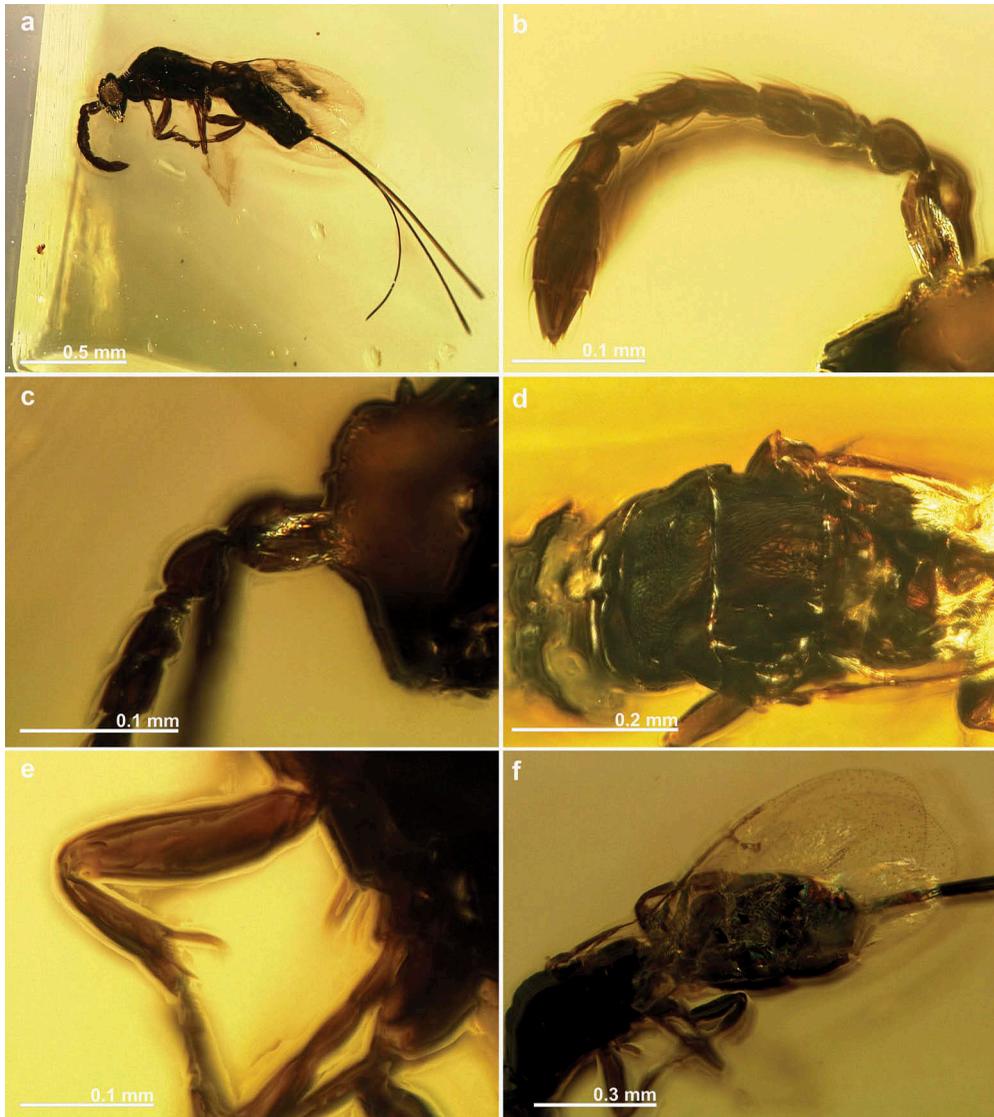


Figure 1. *Idarnes thanatos* sp. nov. female. (a) habitus in lateral view; (b) antenna; (c) detail of antenna; (d) mesosoma in dorsal view; (e) detail of profemur and protibia; (f) wings.

Derivation of name

The specific name is derived from the Greek 'θάνατος', the god of death, in reference to it being an extinct taxon.

Diagnosis

Body colour mostly black, with faint metallic reflection. Antenna with two anelli. Supraclypeal area wider than torulus diameter. Mesoscutum and mesoscutellum reticulate. Postmarginal vein 1.2× as long as stigmal vein. Ovipositor sheaths 1.1× as long as body.

Description

Size and colour. Body length (excluding ovipositor) 1.1 mm. Length of ovipositor sheaths 1.2 mm. Body colour mostly black, with faint metallic reflection, mostly green and orange, at least on mesosoma in dorsal view. Antennae dark brown. Legs yellow brown. Wings hyaline, submarginal vein dark brown, marginal, postmarginal, and stigmal veins light brown.

Head. Antenna with 13 antennomeres including two anelli; antennal formula 11263. Scape 1.4× as long as pedicel. Funicular segments 1.0–1.4× as long as wide. Clava well delimited, with three laterally compressed flagellomeres (compression probably related to *post mortem* alteration). Antennae inserted just above the lower line of compound eyes. Head transverse, 1.3× as wide as high. Head sculpture reticulated, at least close to vertex. Supraclypeal area wider than torulus diameter. Clypeal margin unilobed.

Mesosoma. Pronotum longer than high in lateral view. Mesoscutum and mesoscutellum reticulate. Notauli complete. Mesoscutellar–axillar complex with straight axillular grooves and transverse frenal sulcus, delimitating a square mesoscutellum. Mesoscutellum 1.1× as long as wide. Propodeum length 3.5× propodeal spiracle diameter. Postmarginal vein 1.2× as long as stigmal vein. Protibia with a bifurcated tibial inner spur. Metatibia with two tibial inner spurs.

Metasoma. Suboval. Ovipositor sheaths 1.1× as long as body. Ovipositor teeth concentrated at the distal extremity of ovipositor. Teeth heterogeneously distributed and of variable length, shorter at the tip of the ovipositor.

Measurements (mm). Head: *L* 0.13 *W* 0.28 *H* 0.22; Mesosoma *L* 0.47; Metasoma *L* 0.51. Scape *L* 0.17; Pedicel *L* 0.05; *F*₁ *L* 0.03 *W* 0.03; *F*_{2–6} *L* 0.04 *W* 0.03; Clava *L* 0.11 *W* 0.05; Eye *L* 0.18 *H* 0.22; Profemur *L* 0.2 *W* 0.05; Protibia *L* 0.15 *W* 0.03; Protibial inner spur *L* 0.05; Metafemur *L* 0.18 *W* 0.05; Metatibia *L* 0.17 *W* 0.03; Metatibial inner spur 1 *L* 0.04; Metatibial inner spur 2 *L* 0.03.

Remarks

The (unnamed) specimen was used previously in Cruaud et al. (2011a) for calibration of a molecular clock analysis. *Idarnes thanatos* sp. nov. belongs to the *I. carme* species-group, based on the following characters: (1) postmarginal vein longer than stigmal vein, (2) ovipositor longer than body, (3) clypeal margin unilobed, (4) head sculpturation heterogeneous (but visualization of this character was difficult due to the preservation of the fossil), and (5) ovipositor teeth concentrated at the distal extremity of the ovipositor, with a heterogeneous distribution and of variable length. We are confident that *I. thanatos* sp. nov. does not belong to any known extant *Idarnes* species. This putatively extinct species can be easily distinguished from other known *Idarnes carme* sp. gp species by a combination of characters: (1) the presence of two anelli (rather than one) and (2) its relatively short ovipositor.

Holotype

Female, MZSP, amber from the Dominican Republic. The specimen occurs in a small, clear piece of amber measuring 3.9 mm in length, 2.5 mm in height, and 1.5 mm in width (thickness). The amber piece is attached to a glass holder and mounted on an entomological pin to facilitate handling and image acquisition. The specimen is deposited in the Hymenoptera collection at Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Estimation of host fig size

Body characters and fig diameter across extant *Idarnes* species and their hosts were positively correlated ($R^2 = 0.68-0.76$, $p \leq 10^{-8}$, Table 1). This pattern was also observed when we used maximum fig size instead of median fig sizes, which confirmed the robustness of the median as a measure of size. Ovipositor sheath length was the body

Table 1. Models used to explain fig wasp characters as a function of fig diameter ($N = 31$ pairs of species).

Model	Slope	R ²	t value	Prob.
Ovipositor sheath length ~ fig size	2.9 ± 0.3	0.76	9.69	<10 ⁻⁹
Body length ~ fig size	0.5 ± 0.06	0.69	8.28	<10 ⁻⁸
Ovipositor/body ~ fig size	1.3 ± 0.15	0.70	8.43	<10 ⁻⁸

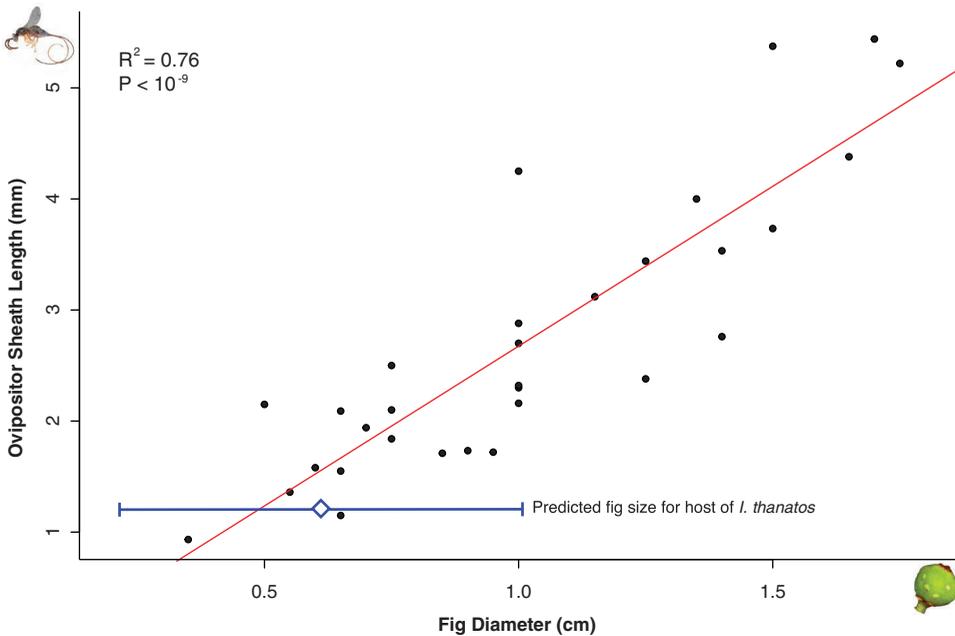


Figure 2. Linear regression between *Idarnes carme* sp. gp ovipositor sheath lengths and median host fig diameters. Lines represent fitted model (red) and fig diameter ±95% CI (blue) for a 1.2 mm ovipositor sheath length, which represents the ovipositor sheath length of *I. thanatos* sp. nov. Each point represents a different fig wasp species and the fig diameter of its host species.

character best explained by fig diameter (Table 1, Figure 2). The fitted value of median fig diameter for the ovipositor sheath length of *I. thanatos* sp. nov. (OL = 1.2 mm) was 0.61 cm (CI_{95%} = 0.22–1.01 cm) (Figure 2). Among the 31 studied fig wasp species, 20 occurred in figs with the same diameter range as the 95% CI calculated for the diameter of the putative host of *I. thanatos*, and comprised the *Ficus americana* and *F. aurea* complexes, some varieties of the *F. pertusa* complex, *F. citrifolia*, *F. cestrifolia*, *F. colubrinae*, *F. eximia*, *F. hartwegii* and *F. mariae*. More specifically, the body length and ovipositor sheath length of *I. thanatos* are similar to those of three *Idarnes* species currently associated with the *F. americana* complex.

Discussion

Palaeontological data obtained from fig wasps is scarce, because so few extinct species have been described, and this has limited the insights they can provide into the evolution of the fig tree–fig wasp system (Peñalver et al. 2006; Compton et al. 2010). Non-pollinating fig wasps are far more diverse and species-rich than pollinators in current fig wasp communities (Compton et al. 1994; Marussich and Machado 2007; Segar et al. 2014). The only putative non-pollinating fig wasp that has been described previously (Barling et al. 2013) does not exhibit any apomorphic characters that confirm it as a chalcid wasp. This makes *Idarnes thanatos* sp. nov. the first confirmed fossil representative of the non-pollinator fig wasps that are so diverse in figs today.

The *I. carme* species-group is the most speciose group of *Idarnes* (Gordh 1975; Cruaud et al. 2011b). They are known to occur throughout most of the distribution of *Ficus* section *Americana*, from southern Brazil to Florida (Gordh 1975). Since they are unable to develop without the pollinator *Pegoscapus* Cameron, they are probably cleptoparasites of this genus of pollinating fig wasps (Elias et al. 2012). Species belonging to this group can be host specific, but some utilize several co-occurring host species (Marussich and Machado 2007). This group was retrieved as monophyletic and sister to the other *Idarnes* species-groups in a global phylogenetic analysis of Sycophaginae (Cruaud et al. 2011b). The molecular clock analyses that used *I. thanatos* as a calibration point (Cruaud et al. 2011a) estimated *Idarnes* to have originated 29.2–18.2 Ma. According to this analysis, *Idarnes* probably arose after the break-up of Gondwanaland, between the Oligocene and Miocene (Cruaud et al. 2011a), a conclusion consistent with its New World distribution. Dominican amber cannot be dated accurately, but *I. thanatos* clearly dates to a period close to the origins of the genus, and indicates that distinct species groups, with differing ecologies, had already diverged by that time. Recent analyses suggested that the ovipositor morphology is correlated with feeding regime (Elias 2013) in *Idarnes* species. *Idarnes thanatos*' ovipositor shows heterogeneously spaced teeth that are shorter near the tip of the ovipositor. This observation is consistent with other morphological features of the *I. carme* sp. gp, and strongly suggests that *I. thanatos* was a cleptoparasite, probably feeding on resources of pollinating fig wasps (Elias 2013).

Correlations between fig wasp morphology and host plant characters are well documented in figs and fig wasps (van Noort and Compton 1996; Kjellberg et al. 2001; Weiblen 2004). For species that oviposit from the outside of figs, the lengths of their ovipositors reflect the size of the figs at the time that they oviposit, which varies depending on their host species, and the stage of fig development when oviposition

takes place (Zhen et al. 2005; Ghara and Borges 2010). Larger figs tend to have thicker walls, and consequently in larger figs the ovules in which most fig wasps develop are located further from the outer surface. Longer ovipositors are therefore required.

Our regression analyses found a strong relationship between ovipositor sheath length and host fig diameter. Based on comparisons using extant fig tree species and their associated *Idarnes* wasps, *Idarnes thanatos* was associated with a small to medium-sized fig with a diameter between 0.2 and 1.0 cm. Measurements taken of *I. thanatos* were most similar to those of a modern *Idarnes* species associated with figs of *Ficus americana* Aubl. (Supplementary File 2), suggesting that the host fig of *I. thanatos* was of similar size. *Ficus americana* figs are eaten by a range of vertebrate frugivores, including doves, passerine birds and primates (Shanahan et al. 2001). The host fig tree of *I. thanatos* may or may not be extinct, but a rather different assemblage of vertebrate species from a similar guild are likely to have been dispersing its seeds at the time when this particular individual became trapped in amber (Herrera 1985).

Acknowledgements

We thank Gunther Fleck for invaluable help and guidelines for imaging and specimen preparation.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

FHAF was supported by FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) [#2010/51158-5, #2012/19815-1 and #2015/06430-2]. RASP was supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) [#306078/2014-7].

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