Systematic Entomology

Systematic Entomology (2013), **38**, 14–34

Taxonomic revision and molecular phylogeny of the fig wasp genus *Anidarnes* Bouček, 1993 (Hymenoptera: Sycophaginae)

FERNANDO H. A. FARACHE[1,*], ASTRID CRUAUD[2,*], GWENAËLLE GENSON[2], RODRIGO A.S. PEREIRA[3] and JEAN-YVES RASPLUS[2]

[1]PPG em Entomologia, Depto de Biologia/FFCLRP-USP Ribeirão Preto, SP, Brazil, [2]INRA-UMR 1062 CBGP (INRA/IRD/CIRAD/SupAgro) Montferrier-sur-Lez, France and [3]Depto de Biologia/FFCLRP-USP Ribeirão Preto, SP, Brazil

Abstract. Besides the pollinators (Agaonidae), several chalcidoid lineages of nonpollinating fig wasps are strictly dependent on *Ficus* (Moraceae) for reproduction. Overall, nonpollinating fig wasps have not received much consideration. Reliable phylogenetic and taxonomic frameworks are lacking for most groups, which hampers progress in our understanding of the evolution and functioning of fig wasp communities. Here we focus on *Anidarnes* Bouček (Sycophaginae), a member of the Neotropical fig wasp community. We present a detailed morphological analysis as well as the first molecular phylogeny of the genus inferred from two nuclear and two mitochondrial genes (*Cytb*, *COI*, *EF-1α* and 28S rRNA, 3937 bp). Twelve species are recognised, illustrated and a key to their identification is provided. Of those, only three were previously described and are redescribed here: *A. bicolor* (Ashmead); *A. globiceps* (Mayr) and *A. brevicauda* Bouček. In addition, nine new species are described: *Anidarnes brevior* **sp.n.** Farache & Rasplus (Costa Rica); *A. dissidens* **sp.n.** Farache & Rasplus (Brazil); *A. gracilis* **sp.n.** Farache & Rasplus (Costa Rica); *A. isophlebiae* **sp.n.** Farache & Rasplus (Costa Rica); *A. jimeneziae* **sp.n.** Farache & Rasplus (Costa Rica); *A. longiscutellum* **sp.n.** Farache & Rasplus (Brazil); *A. martinae* **sp.n.** Farache & Rasplus (U.S.A., Florida); *A. nigrus* **sp.n.** Farache & Rasplus (Colombia) and *A. rugosus* **sp.n.** Farache & Rasplus (Brazil). Finally, phylogenetic relationships inferred using parsimony, bayesian and maximum likelihood methods are discussed in the light of our morphological observations and the host fig tree taxonomy.

Introduction

Every species of fig tree (*Ficus*, Moraceae) hosts a unique assemblage of fig wasps that reproduce exclusively within the fig fruit, or syconium, which is an enclosed inflorescence (Janzen, 1979). Pollinating fig wasps (Chalcidoidea: Agaonidae), in turn, pollinate the fig tree, and neither partner of the fig–fig wasp mutualism can complete its lifecycle without the other (Weiblen, 2002; Cook & Rasplus, 2003). Besides Agaonidae, several chalcidoid lineages of nonpollinating fig wasps also utilise the fig syconia as oviposition sites (West *et al.*, 1996; Kerdelhué *et al.*, 2000; Cook & Rasplus, 2003). Among them are the Sycophaginae. This subfamily occurs in all tropical regions of the world and is associated with two unrelated subgenera of *Ficus*, namely *Urostigma* and *Sycomorus* (Wiebes, 1966; Cruaud *et al.*, 2011a). To date, Sycophaginae comprises 5 genera and 52 described species (Cruaud *et al.*, 2011b). However, the diversity of the subfamily is estimated at 700 species, suggesting that more than 90% of the species await description. Bouček (1988) assigned

Correspondence: Fernando Henrique Antoniolli Farache, Depto. de Biologia/FFCLRP, Universidade de São Paulo, Av. Bandeirantes 3900, Ribeirão Preto, SP 14040-900, Brazil. E-mail: fhafarache@gmail.com

*These authors contributed equally to this work.

© 2013 The Royal Entomological Society

Sycophaginae and other fig wasp subfamilies to Agaonidae (fig pollinators) based mostly on the presence of a postgenal bridge on the back of the head and by their strict association with *Ficus* syconia. Rasplus *et al.* (1998) re-examined the monophyly of Agaonidae *sensu* Bouček using molecular characters and proposed to restrict the family to the pollinator clade but did not assign the Sycophaginae to family. However, an ongoing phylogenetic study of Chalcidoidea combining morphological and molecular data places them as sister to the Agaonidae, where they could be placed again (J.M. Heraty *et al.*, in preparation). Overall, neotropical fig wasps have received little taxonomic attention, and few species have been described. Agaonids have been mostly described by G. Mayr, G. Grandi and W. Ramirez, and the group was revised by Wiebes (1995). Nonpollinating fig wasps are even less well known, and few publications (Gordh, 1975; Mayr, 1885; Bouček, 1993) deal with neotropical Sycophaginae. Thus, evolutionary and ecological studies of fig wasps in the Neotropics are mostly based on insufficient taxonomic background (West & Herre, 1994; West *et al.*, 1996; Marussich & Machado, 2007).

Neotropical Sycophaginae belong to two not closely related genera (Cruaud *et al.*, 2011b), namely *Idarnes* Walker and *Anidarnes* Bouček, which have not been intensively sampled and remain poorly studied (Gordh, 1975; Bouček, 1993). *Anidarnes* was first recognised by Bouček (1993) and included only three species. However, recent estimates suggest that *Anidarnes* may include about 20 species (Cruaud *et al.*, 2011b), although this number may be an underestimate.

According to Cruaud *et al.* (2011b), *Anidarnes* belongs to a clade of Sycophaginae that could be treated as a tribe together with the Australasian *Pseudidarnes* and an undescribed Oriental genus (referred to here as 'undescribed genus'). *Pseudidarnes* appears sister to *Anidarnes* + undescribed genus. A recent biogeographic analysis also suggested that the ancestor of *Anidarnes* + undescribed genus may have dispersed from Australasia to Sundaland about 25–20 Ma. Subsequently, *Anidarnes* probably reached the New World via the North Atlantic land bridges during the late Oligocene warming event (Cruaud *et al.*, 2011a).

Anidarnes wasps develop in figs of the *Ficus* section *Americana* (subgenus *Urostigma*), which are all pollinated by *Pegoscapus* species (Agaonidae). Very little is known about the biology of *Anidarnes,* and only the natural history and ecology of *A. bicolor* has been described with some detail (Bronstein, 1999). *Anidarnes* species are the earliest gall-inducers that oviposit through the syconium wall before pollination (Cruaud *et al.*, 2011b). They have short and thick ovipositors (shorter than their body lengths) relative to other Sycophaginae ovipositing in the same syconia. *Anidarnes* larvae develop in large galls that appear to be rotund invaginations of the inner wall of the fig (Bronstein, 1999). When numerous, these large galls can occupy nearly the entire volume of the syconium. In *Ficus aurea* about one third of the sampled figs contains *Anidarnes* galls with an average of 5.4 ± 4.4 (mean ± SD) *Anidarnes* galls per fig (Bronstein, 1999). However, other *Anidarnes* species are less common, making it difficult to sample enough specimens for systematic study. *Anidarnes bicolor* only matures in pollinated figs and has a distinctly negative effect on the pollinator offspring. Possible explanations may be that *Anidarnes* galls crush pollinator galls as they develop or draw away fig resources that are otherwise available to pollinator galls (Bronstein, 1999). As with most sycophagine wasps exhibiting large galls and small brood size, all known *Anidarnes* possess only winged males. Consequently, mating probably occurs outside of the fig.

The purpose of this paper is to provide a systematic review of *Anidarnes* based on morphological and molecular data. All currently recognised species are redescribed and nine new species are described. All species are illustrated and a key to their identification is presented. To infer phylogenetic relationships among *Anidarnes* species, we also conduct Bayesian, likelihood and parsimony-based analyses of four genetic loci (*Cytb*, *COI*, *EF-1α* and 28S rRNA) and discuss the results in the light of our morphological observations and the host fig tree taxonomy.

Material and methods

Specimen collection

Figs were collected before maturity and transferred to tissue bags until wasp emergence. Wasps were killed using acetate (or freezing) and placed into 70% ethanol. Wasps used for molecular analysis were subsequently stored in 95% ethanol until extraction. Geographical coordinates and altitude were recorded in the field with a GPS device or estimated using label information.

Morphological study

Morphological terminology follows Gibson (1997). Abbreviations for measurements used in the text include: POL, distance between posterior ocelli; OOL, distance between posterior ocellus and eye margin.

Abbreviations for repositories follow Arnett *et al.* (1993):

BMNH. The Natural History Museum, London, U.K.
CBGP. Centre de Biologie pour la Gestion des Populations, Montpellier, France.
MZSP. Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
NMW. Naturhistorisches Museum, Wien, Austria.
SAMC. Iziko South African Museum, Cape Town, South Africa.
USNM. National Museum of Natural History, Washington D.C., U.S.A.

Illustrations. Field-collected specimens were dehydrated through an ethanol and HMDS series (Heraty & Hawks, 1998) or critical point dried (BAL-TEC CPD 030') before card mounting. Images of specimens were produced with an EntoVision Premium Portable Imaging System, comprising 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 U.S.A.). Cartograph v5.6.0 (Microvision, Evry, France) software was subsequently used to merge an image series (representing about ten focal planes), producing a single image with increased depth of field. Some specimens were dissected, mounted and sputter-coated with gold for scanning electron microscopy (SEM), which was performed with a Zeiss EV050 or Shimadzu SS-550 microscope. Type specimens were photographed using low vacuum Quanta 250 FEG Scanning Electron Microscope. Images were assembled and processed using Adobe Photoshop CS4© software.

Molecular study

Taxonomic sampling. Phylogenetic relationships among ten of the twelve *Anidarnes* species were inferred using sequence data from two specimens per species. Single individuals belonging to other sycophagine genera were used as outgroups following Cruaud *et al.* (2011a): undescribed genus sp. ex *F. sumatrana*, *Eukoebelea* sp. ex *F. glandifera*, *Idarnes* sp. ex *F. americana* (*F. perforata*) and *Pseudidarnes* sp. ex *F. baola* (Table 1).

Laboratory protocols. Genomic DNA was isolated using Qiagen DNeasy kit following the manufacturer's protocol but without destruction of the specimens. Vouchers were deposited at CBGP, Montferrier-sur-Lez, France. We sequenced one nuclear protein-coding gene, F2 copy of elongation factor-1α (*EF-1α*), two mitochondrial protein-coding genes [cytochrome c oxidase subunit I (*COI*), cytochrome b (*Cyt b*)], and the ribosomal 28S rRNA (D2–D3 and D4–D5 expansion regions). Primer sequences and amplification protocols followed Cruaud *et al.* (2010) for *Cytb, COI* and 28S rRNA and Cruaud *et al.* (2011a) for *EF-1α*. PCR products were purified using ExonucleaseI and Phosphatase, and sequenced directly using the BigDyeTerminator v3.1 kit (Applied Biosystems) and an ABI3730XL sequencer at Genoscope, Evry, France. Both strands for each overlapping fragment were assembled using the sequence editing software Geneious v5.5.7 (Drummond *et al.*, 2010). All sequences were deposited in GenBank (Table 1).

Phylogenetic analyses. All gene regions were aligned with MAFFT v6.864 (Katoh *et al.*, 2005) using the L-INS-i option. Alignments of protein coding genes were translated to amino acids using MEGA v4 (Tamura *et al.*, 2007) to detect frame-shift mutations and premature stop codons, which may indicate the presence of pseudogenes.

Parsimony analyses were conducted using TNT v1.1 (Goloboff *et al.*, 2008), using New Technology Search: 1000 replicates of random addition sequences (RAS), followed by random sectorial searches with default options, 20 cycles of ratchet and three rounds of tree-fusing. All substitutions were equally weighted and gaps treated as a missing data. Robustness of topologies was assessed by bootstrap procedures using 1000 replicates. Bootstrap percentages (BP) $\geq$ 70% were considered strong support.

Maximum likelihood (ML) and Bayesian analyses were conducted using the partitioned dataset and implementing separate nucleotide substitution models for subsets of the data more likely to have experienced similar evolutionary processes (mitochondrial genes, *EF-1α*, rRNA). The most appropriate model of gene evolution for each data partition was identified using the Akaike information criterion implemented in MrAIC.pl 1.4.3 (Nylander, 2004).

We performed ML analyses and associated bootstrapping using MPI-parallelised RAxML v7.2.8. (Stamatakis, 2006). GTRCAT approximation of models was used for ML bootstrapping (Stamatakis, 2006) (1000 replicates).

Bayesian analyses were conducted using a parallel version of MrBayes v3.1.1. (Huelsenbeck & Ronquist, 2001). We assumed across-partition heterogeneity in model parameters by considering the parameter m. Parameter values for the model were initiated with default uniform priors and branch lengths were estimated using default exponential priors. To improve mixing of the cold chain and prevent it from becoming trapped in local optima, we used Metropolis-coupled Markov chain Monte Carlo (MCMC) with each run including a cold chain and three incrementally heated chains. The heating parameter was set to 0.02 in order to allow swap frequencies from 20 to 70%. We performed two independent runs of one million generations. All values were sampled every 1000 generations. For the initial determination of burn-in, we examined the plot of overall model likelihood against generation number to find the point where the likelihood started to fluctuate around a constant value. The points sampled prior to convergence of the chains were then discarded. Convergence was also evaluated using Tracer v1.5 (Rambaut & Drummond, 2004). The results were based on the pooled samples from the stationary phases of the two independent runs. Posterior probabilities (PP) $\geq$ 0.95 were considered as strong support and PP $<$ 0.90 as weak.

Results

Phylogenetic position of Anidarnes and key to genera

Anidarnes belongs to a small clade (not named) of Sycophaginae (see Cruaud *et al.*, 2011b), which is well-characterised by the following combination of characters: (i) mesosoma high and robust, arched, not flattened dorsoventrally (with the exception of one species belonging to the undescribed genus); (ii) notauli deep and transversely crenulated, axillular and frenal grooves all conspicuous (with the exception of one species belonging to the undescribed genus); (iii) metascutellum conspicuous and r elatively well delimited (Fig. 1B); (iv) clypeal margin bilobed, but this character is also shared with other species (Fig. 1E); (v) winged males, shared

Table 1. List of *Anidarnes* and outgroup species included in the molecular analysis. Voucher numbers, taxonomic information, host *Ficus* species, locality data and Genbank accession numbers.

Voucher number	Species	Host *Ficus* species	Locality	*COI*	*Cytb*	*EF-1α*	28S rRNA
1680_01w01x	*Anidarnes niger*	*F. andicola*	Colombia, Cundinamarca, Bogota D.C., Ciudad Universitaria	JQ925908	JQ925894	JQ925875	JQ925926
2085_02w01a	Undescribed genus sp.	*F. sumatrana*	Indonesia, Sulawesi, Pattunuang	HM770620	HM770576	HM770522	HM770682
2171_01w01a	*Anidarnes gracilis*	*F. trachelosyce*	Costa Rica, Pequena Helvetia, Hotel Los Heroes	JQ925909	JQ925895	JQ925876	JQ925927
2171_01w01c	*Anidarnes gracilis*	*F. trachelosyce*	Costa Rica, Pequena Helvetia, Hotel Los Heroes	JQ925910	JQ925896	JQ925877	JQ925927
2177_02w01b	*Anidarnes brevior*	*F. americana*	Costa Rica, Pequena Helvetia, Hotel Los Heroes	JQ925911	Ø	JQ925878	JQ925928
2177_02w01c	*Anidarnes brevior*	*F. americana*	Costa Rica, Pequena Helvetia, Hotel Los Heroes	JQ925912	Ø	JQ925879	JQ925928
2177_03w01a	*Idarnes* sp.	*F. americana*	Costa Rica, Pequena Helvetia, Hotel Los Heroes	HM770625	HM770579	HM770527	HM770687
2181_03w01a	*Anidarnes jimeneziae*	*F. jimenezii*	Costa Rica, Santo Dominguo de Heredia	JQ925913	JQ925897	JQ925880	JQ925929
2181_03w01b	*Anidarnes jimeneziae*	*F. jimenezii*	Costa Rica, Santo Dominguo de Heredia	JQ925914	JQ925898	JQ925881	JQ925929
2523_02w011	*Pseudidarnes* sp.	*F. baola*	Solomon Islands, Gatokae, Mbulo island	HM770640	HM770594	HM770543	HM770702
2529_01w013	*Eukoebelea* sp.	*F. glandifera*	Solomon Islands, Gatokae, Mbulo island	HM770641	HM770595	HM770544	HM770703
2573_02w013	*Anidarnes longiscutellum*	*F. eximia*	Brazil, Sao Paulo	JQ925915	JQ925899	JQ925882	JQ925930
2573_02w01a	*Anidarnes longiscutellum*	*F. eximia*	Brazil, Sao Paulo	JQ925916	JQ925900	JQ925883	JQ925930
2578_02w013	*Anidarnes rugosus*	*F. crocata*	Brazil, Sao Paulo, Teodoro Sampaio	JQ925917	Ø	JQ925884	JQ925931
2578_02w01a	*Anidarnes rugosus*	*F. crocata*	Brazil, Sao Paulo, Teodoro Sampaio	JQ925918	JQ925901	JQ925885	JQ925931
2586_02w013	*Anidarnes dissidens*	*F. obtusifolia*	Brazil, Sao Paulo, Galia	JQ925919	Ø	JQ925886	JQ925932
2586_02w01a	*Anidarnes dissidens*	*F. obtusifolia*	Brazil, Sao Paulo, Galia	JQ925920	JQ925902	JQ925887	JQ925932
2824_02w011	*Anidarnes isophlebiae*	*F. isophlebia*	Costa Rica, Puerto Viejo de Talamanca	JQ925921	JQ925903	JQ925888	JQ925933
2824_02w01a	*Anidarnes isophlebiae*	*F. isophlebia*	Costa Rica, Puerto Viejo de Talamanca	Ø	JQ925904	JQ925889	JQ925933
2871_03w01a	*Anidarnes martinae*	*F. aurea*	U.S.A., Florida, Florida City, NW 14th St	JQ925922	JQ925905	JQ925890	JQ925934
2871_03w01b	*Anidarnes martinae*	*F. aurea*	U.S.A., Florida, Florida City, NW 14th St	JQ925923	JQ925906	JQ925891	JQ925934
2874_03w012	*Anidarnes bicolor*	*F. aurea*	U.S.A., Florida, Everglades	JQ925924	Ø	JQ925892	JQ925935
2874_03w01b	*Anidarnes bicolor*	*F. aurea*	U.S.A., Florida, Everglades	JQ925925	JQ925907	JQ925893	JQ925935

with *Idarnes incerta* group and few *Eukoebelea* species. The genera included in this clade can be identified using the following key:

1. Female with long petiole, at least as long as broad (Fig. 1A). Maxillary palpi composed of four segments (Fig. 1C). Labial palpi composed of three segments (Fig. 1C). Hypopygial projection (mucro) relatively long. Postmarginal vein conspicuous, longer than thick. Associated with *Ficus* subgenus *Urostigma* section *Stilpnophyllum*. Australasia .... ***Pseudidarnes* Girault, 1927**

– Female with short and transverse petiole (Fig. 1B). Maxillary and labial palpi composed at most of two segments, the last one frequently reduced and setae-like (Fig. 1D). Mucro short, triangular, with the exception of *A. dissidens*. Postmarginal vein very short, inconspicuous; sometimes absent. **2**

2(1) Mesosoma with metallic tinge. Interantennal projection absent. Toruli close together, touching each other (Fig. 1F).

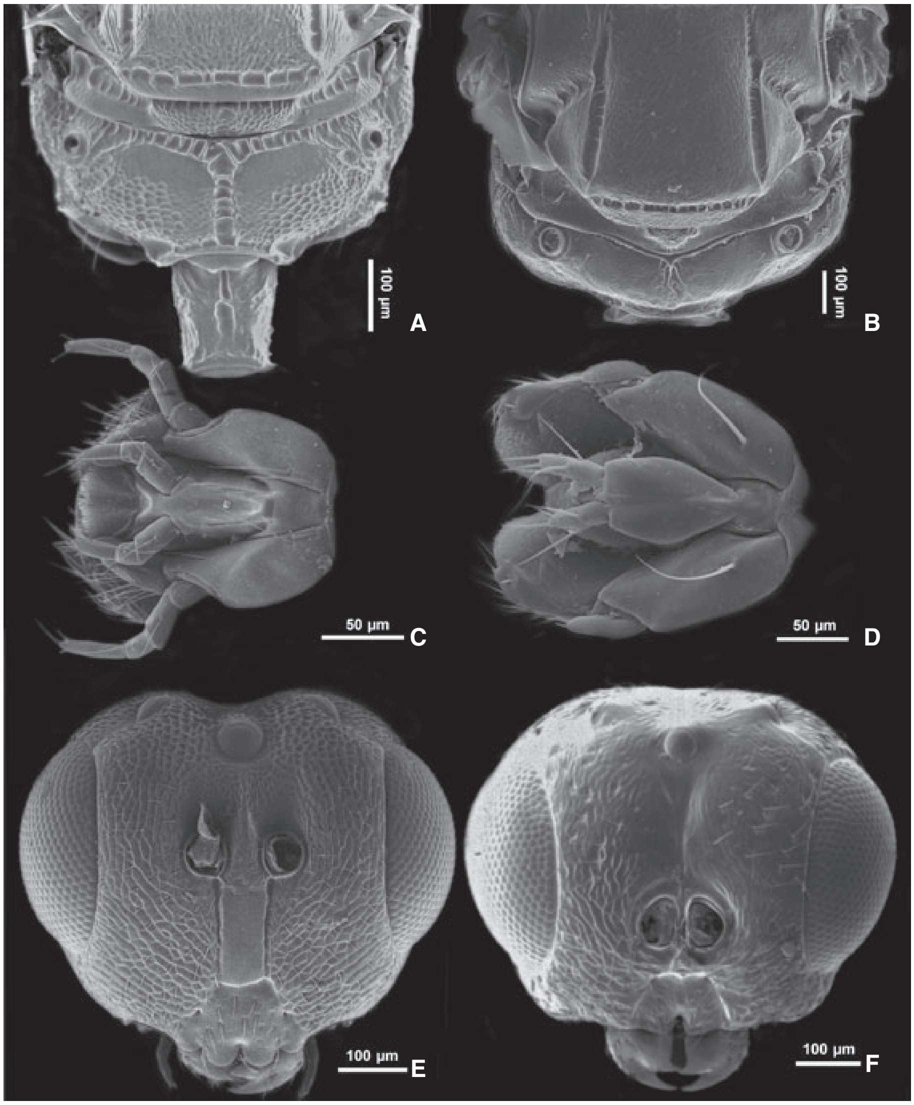

Fig. 1. (A) *Pseudidarnes*, mesosoma and petiole (ex. *F. obliqua*, Australia); (B) *A. dissidens* **sp.n.,** mesosoma and petiole.; (C) *Pseudidarnes minerva* Girault, labiomaxillary complex; (D) *Anidarnes longiscutellum* **sp.n.,** labiomaxillary complex; (E) *Pseudidarnes* sp. (ex. *F. obliqua*, Australia), head (front); (F) undescribed genus sp. (ex. *F. altissima*, China), Head (front).

Supraclypeal area about the same size as clypeus height (measured from a line drawn between the tentorial pits to the ventral margin of the toruli), depressed laterally, poorly delimited (Fig. 1F). Antennae inserted in the middle of the face, rarely above (one species) (Fig. 1F). Associated with *Ficus* subgenus *Urostigma* section *Conosycea*. South East Asia, China .... undescribed genus.
– Mesosoma without metallic tinge, generally black to yellow (only *A. martinae* with metallic head). Inter-antennal projection conspicuous, in one species as a small triangular callus (Fig. 4J). Toruli separated by at least half their own diameter. Supraclypeal area longer than clypeus height, flattened, laterally well delimitated by sulcus or line. Associated with *Ficus* subgenus *Urostigma* section *Americana*. South and Central America, Florida .... ***Anidarnes* Bouček, 1993**

***Anidarnes* Bouček, 1993**

Type species: *Sycophila bicolor* Ashmead, 1900 by monotypy.

Generic diagnosis. Head transverse (1.2–1.7× as wide as high). Maxillary and labial palpi composed at most of two segments, the last one frequently reduced and setae-like (Fig. 1D). Antennae inserted closer to the median ocellus than to the clypeal margin. Toruli separated by at least half their own diameter. Supraclypeal area longer than clypeus height, flattened, laterally well delimited by sulcus or line. Antennae with 12 flagellomeres (14 antennomeres), 12th flagellomere very small. Mesosoma without metallic tinge, generally black to yellow, curved dorsally. Mesoscutellum rectangular. Marginal vein very short, stub-like to absent. Ovipositor sheaths always shorter than metasoma, almost always with a median constriction and depigmentation.

Female. Body length 1.7–3.5 mm. Head usually without metallic tinge (excepted *A. martinae* **sp.n.** Farache & Rasplus), transverse (1.2–1.7× as wide as high). Antennae inserted closer to the median ocellus than to the clypeal margin. Torulus separated by one torulus diameter or less, but never closer than 0.5× torulus diameter. Clypeal margin bilobed. Clypeus as broad as high or broader than high (0.9–2.4× as broad as high). Scrobal cavity including median ocellus. Labial and maxillary palpus both one or two-segmented (apical segment small, stub-like). Face sculpture smooth to reticulate, never punctate. Supraclypeal area always delimited laterally by subantennal groove. Interantennal projection usually lanceolate or triangular (flat and long in *A. dissidens* **sp.n.** Farache & Rasplus). Vertex at least slightly concave. Antenna usually with two anelli (*A. martinae* Farache & Rasplus with one anellus). Antennae with 12 flagellomeres (14 antennomeres), 12th flagellomere very small, almost as broad as high or elongate. Clava mostly not distinctly differentiated.

Mesosoma never metallic, curved dorsally. Pronotum smooth or slightly reticulated. Notauli deep and more or less crenulated. Prosternum round at the posterior margin, with a median discrimen or line, almost reaching the anterior part of the sclerite. Axilullar sulcus straight to slightly concave. Frenal sulcus transverse, slightly concave. Mesoscutellum nearly rectangular. Metascutellum small, rectangular or trapezoidal, inconspicuous in *A. globiceps* (Mayr), and triangular in *A. dissidens* **sp.n.** Farache & Rasplus. Propodeum never separated from metanotum by a long peduncle. Marginal vein very short, stub-like to absent. Stigmal vein as long as marginal vein or slightly longer.

Metasoma sessile. Ovipositor sheaths always shorter than metasoma, almost always with a median constriction and depigmentation (constriction and depigmentation absent in *A. dissidens* **sp.n.** Farache & Rasplus).

Male. Similar to female, usually showing tinge variation. Flagellomeres slightly longer. 12th antennomere more conspicuous. Body slender.

Note. In our opinion, *Idarnes* (the root of *Anidarnes*) is derived from *Hydarnes* (Greek: Ὑδάρνης; Latin: *Idarnes*), a Persian general that fought the Greeks at Thermopylae in 480 BC and commanded the ‘Ten Thousand Immortals’ during the time of king Xerxes’ invasion of Greece. Consequently, *Idarnes* and *Anidarnes* are of masculine gender despite the recurrent use of neuter gender by several authors.

Species descriptions

Anidarnes bicolor (Ashmead, 1900)

(Figs 2A, 3A, 4A, 5A, 6A, 7A)

1900 Ashmead, W.H., *Transactions of the Entomological Society of London* 33: 252, 335. Description (♀♂) (comb.: *Sycophila bicolor*)

1993 Bouček, Z., *Journal of Natural History* 27: 200. Combination, lectotype designation (comb.: *Anidarnes bicolor*)

1999 Bronstein, J.L., *Florida Entomologist* 82: 454-461. Biology (comb.: *Anidarnes bicolor*)

2011 Cruaud, A. *et al.*, *BMC Evolutionary Biology* 11: 8. Phylogenetic positon (comb.: *Anidarnes bicolor*)

Type material. Lectotype ♀, U.S.A., Florida, Cocoanut Grove, E.A. Schwarz leg. (USNM, examined). Paralectotypes 9♀ 6♂, same data.

Species re-descriptions and non-type materials analysed. See Appendix S1.

Host plant. Ficus aurea Nuttall.

Anidarnes brevicauda Bouček, 1993

(Figs 2B, 3B, 4B, 5B, 6B, 7B)

1993 Bouček, Z., *Journal of Natural History* 27: 200. Description (♀)

Type material. Holotype ♀. Costa Rica, San José Prov. San Pedro de Montes de Oca, 1100 m, ex *F. costaricana,* April 1991, P. Hanson leg. (BMNH, examined). Paratypes: 2 ♀, same data (examined).

Species re-descriptions. See Appendix S1.

Host plant. Ficus costaricana (Liebmann) Miquel.

Anidarnes brevior Farache & Rasplus sp.n.

(Figs 2C, 3C, 4C, 5C, 6C, 7C)

Type material. Holotype ♀ : Costa Rica, Pequena Helvetia, Hotel Los Heroes (10.475466°–84.830086°), 5.3.2008, ex *F. americana* (*perforata*), n°JRAS2177_02, W. Ramirez & JY Rasplus leg. (CBGP). Paratypes: 25♀ 22♂ same data (21♀ 18♂ CBGP, 1♀ 1♂ BMNH, 1♀ 1♂ SAMC, 2♀ 2♂ MZSP).

Etymology. The specific name refers to the short ovipositor of the female.

Diagnosis. Predominantly dark brown. Pronotum yellow brown. Face with long and dense pilosity (Fig. 5C). Interantennal projection short, not exceeding the torulus by one torulus diameter. First funicular segment 0.7–0.9× as long as wide. Notauli, axillular and frenal grooves smooth or shallowly crenulated. Mesoscutellum trapezoidal, the lateral sides diverging posteriorly. Propodeal median line absent. Ovipositor shorter than hind tibia, with median constriction.

Female. Body length 2–2.2 mm. Ovipositor length 0.3–0.4 mm. Predominantly dark brown. Scape and pedicel yellow. Funicle yellow brown. Pronotum yellow brown. Legs brown, foretibia and tarsi yellow. Wings hyaline.

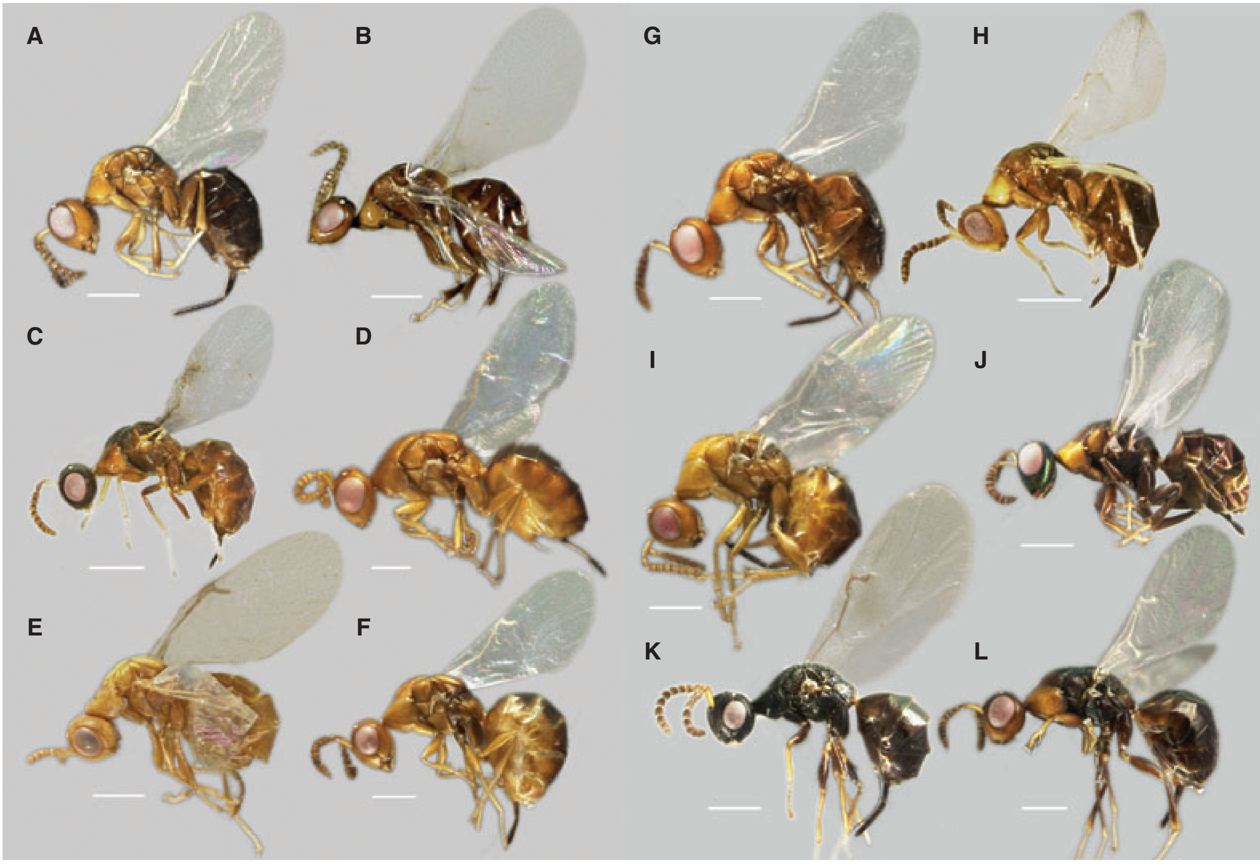

Fig. 2. Habitus of female *Anidarnes* species. (A) *A. bicolor* (Ashmead); (B) *A. brevicauda* Bouček; (C) *A. brevior* **sp.n.**; (D) *A. dissidens* **sp.n.**; (E) *A. globiceps* (Mayr); (F) *A. gracilis* **sp.n.**. (G) *A. isophlebiae* **sp.n.**; (H) *A. jimeneziae* **sp.n.**; (I) *A. longiscutellum* **sp.n.**; (J) *A. martinae* **sp.n.**; (K) *A. nigrus* **sp.n.**; (L) *A. rugosus* **sp.n.**. Scale = 500 µm.

Head. Face reticulate. Pilosity long and conspicuous. Clypeus 1.4× as broad as high. Malar sulcus absent. Epistomal groove shallow. Supraclypeal area broad, wider than 0.5× torulus diameter, faintly reticulate. Subantennal groove shallow and smooth. Interantennal projection triangular, slightly lanceolate and short, exceeding the torulus by less than 1× torulus diameter. Distance from torulus to median ocellus 0.2–0.3× distance from torulus to oral margin. Distance between toruli equal to torulus diameter. Scape length 2.1× pedicel length. Funicle with two anelli. First funicular segment 0.7–0.9× as long as wide. 12th flagellomere quadrate. POL 3.2–3.6× OOL. Vertex slightly concave. Median groove on vertex conspicuous.

Mesosoma. Anterior half of mesoscutum smooth, posterior half engraved. Notauli faintly crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.3× as long as wide, with engraved sculpture. Frenal sulcus smooth. Frenum length *c*. 0.5× metascutellum length. Metascutellum rectangular, striate, without basal crenulation. Propodeal median line absent. Propodeal spiracle separated from the hind margin of metanotum by less than its own diameter. Wings with short and sparse pilosity. Postmarginal vein absent.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 0.8× hind tibia length.

Relative measurements. See Appendix S2.

Male. Similar to female, flagellomeres slightly longer than in females. 12th flagellomere elongate. Wings medially infuscate, with long and dense pilosity.

Host plant. Ficus americana Aublet.

Anidarnes dissidens **Farache & Rasplus sp.n.**
(Figs 2D, 3D, 4D, 5D, 6D, 7D)

Type material. Holotype ♀: Brazil, São Paulo, Gália (−22.373384°−49.669503°), 26.9.2008, ex. *F. obtusifolia*, n°05-5. RAS Pereira & al. leg. (CBGP).

Paratypes: 4♀, Brazil, São Paulo, Gália, (−22.336327°−49.6345°), 31.3.2008, ex. *F. obtusifolia*, n°014-4, FHA Farache & al. leg (CBGP, BMNH, SAMC, MZSP); 2♀, Brazil, São Paulo, Ribeirão Preto (−21.172676°−47.802532°), 24.4.2007,

Fig. 3. Head (front) of female *Anidarnes* species. (A) *A. bicolor* (Ashmead); (B) *A. brevicauda* Bouček; (C) *A. brevior* **sp.n.**; (D) *A. dissidens* **sp.n.**; (E) *A. globiceps* (Mayr); (F) *A. gracilis* **sp.n.**; (G) *A. isophlebiae* **sp.n.**; (H) *A. jimeneziae* **sp.n.**; (I) *A. longiscutellum* **sp.n.**; (J) *A. martinae* **sp.n.**; (K) *A. nigrus* **sp.n.**; (L) *A. rugosus* **sp.n.**. Scale = 100 μm.

ex *F. obtusifolia*, n°147-1, FHA Farache leg. (CBGP); 2♀ Brazil, São Paulo, Gália (−22.3363°−49.6345°), 29.8.2011, ex. *F. obtusifolia*, n° 252-1, LP Rocha leg. (CBGP); 1♂, Brazil, São Paulo, Ribeirão Preto (−21.172676°−47.802532°), 2.7.2006, ex. *F. obtusifolia*, n°134-4, FHA Farache & VT Ó leg. (CBGP); 1♀ Brazil, São Paulo, Gália (−22.303386°−49.746440°), 28.9.2007, ex. *F. obtusifolia*, n°07-1, RAS Pereira & al. leg. (CBGP); 1♀ 3♂, Brazil, São Paulo, Gália (−22.370418°−49.659743°), 31.3.2008, ex. *F. obtusifolia*, n°011-13, FHA Farache & al. leg. (CBGP); 1♀, Brazil, São Paulo, Gália (−22.378522°−49.719124°), 9.7.2009, ex. *F. obtusifolia*, n°155-16, LMR Teixeira leg. (CBGP); 2♀ 3♂, Brazil, São Paulo, Gália (−22.249083° −49.830165°), 10.2.2009, ex. *F. obtusifolia*, n°88-6, FHA Farache leg (2♀ CBGP, 1♂ BMNH, 1♂ SAMC, 1♂ MZSP).

Etymology. The specific name refers to the combination of unusual characters exhibited by this species.

Diagnosis. Predominantly yellow orange. Metasoma dorsally dark brown-black. Interantennal process flat, longer than

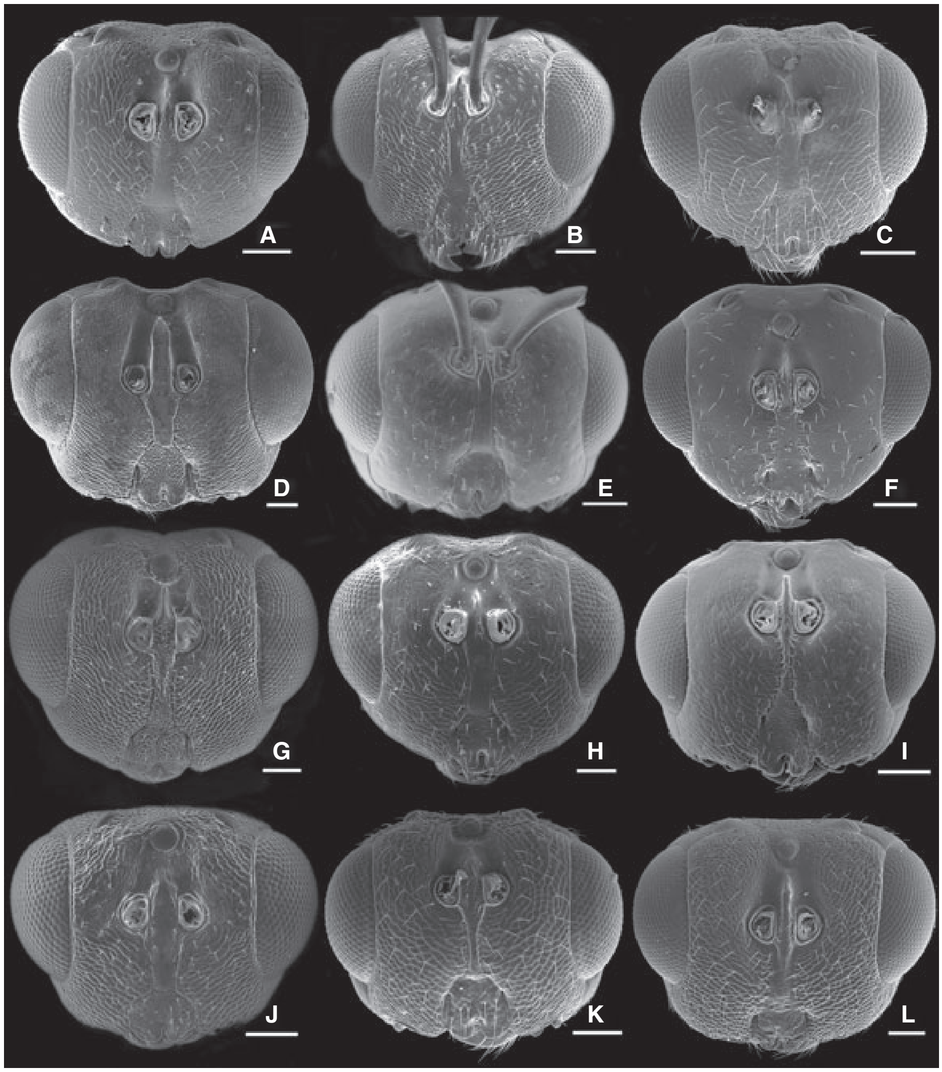

Fig. 4. Antenna of female *Anidarnes* species. (A) *A. bicolor* (Ashmead); (B) *A. brevicauda* Bouček; (C) *A. brevior* **sp.n.**; (D) *A. dissidens* **sp.n.**; (E) *A. globiceps* (Mayr); (F) *A. gracilis* **sp.n.**; (G) *A. isophlebiae* **sp.n.**; (H) *A. jimeneziae* **sp.n.**; (I) *A. longiscutellum* **sp.n.**; (J) *A. martinae* **sp.n.**; (K) *A. nigrus* **sp.n.**; (L) *A. rugosus* **sp.n.**. Scale = 100 μm.

2× torulus diameter (Fig. 3D). Median groove on vertex absent. Metascutellum triangular. Hypopygium apex (mucro) long and narrow (Fig. 2D). Ovipositor without median constriction and depigmentation (Fig. 2D) as long as 1.1× hind tibia length.

Female. Body length 2.8–3.1 mm. Ovipositor length 0.7–0.8 mm. Predominantly yellow orange. Scape and pedicel yellow. Funicle yellow orange. Face yellow. Wings hyaline. Metasoma dorsally dark brown-black.

Head. Face shallowly reticulate. Pilosity short and sparse. Clypeus 1.6× as broad as high. Malar sulcus absent. Epistomal groove present, delimiting clypeus dorsally. Supraclypeal area broad, wider than 0.5× torulus diameter, predominantly smooth. Subantennal groove deep. Interantennal projection flat and very long, exceeding the torulus by almost 2× torulus diameter. Distance from torulus to median ocellus 0.5–0.6× distance from torulus to oral margin. Distance between toruli equal to torulus diameter. Scape length 4.2× pedicel length. Funicle with two anelli. First funicular segment 0.5–0.6× as long as wide. 12th flagellomere elongate. POL 2.2–2.8× OOL. Vertex clearly concave. Median groove on vertex absent.

Mesosoma. Mesoscutum slightly engraved. Notauli densely crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.4–1.6× as long as wide. With faintly engraved sculpture. Frenal sulcus densely crenulate. Frenum length *c.* 1× metascutellum length. Metascutellum triangular, reticulate, without basal crenulation. Propodeal median line present as longitudinal striae. Propodeal spiracle not separated

Fig. 5. Mesosoma of female *Anidarnes* species (Entovision). (A) *A. bicolor* (Ashmead); (B) *A. brevicauda* Bouček; (C) *A. brevior* **sp.n.**; (D) *A. dissidens* **sp.n.**; (E) *A. globiceps* (Mayr); (F) *A. gracilis* **sp.n.**; (G) *A. isophlebiae* **sp.n.**; (H) *A. jimeneziae* **sp.n.**; (I) *A. longiscutellum* **sp.n.**; (J) *A. martinae* **sp.n.**; (K) *A. nigrus* **sp.n.**; (L) *A. rugosus* **sp.n.**. Scale = 200 µm.

from hind margin of metanotum. Wings with short and sparse pilosity. Postmarginal vein present, but short.

Metasoma. Mucro long and narrow. Ovipositor without median constriction. Ovipositor length 1.1× hind tibia length.

Relative measurements. See Appendix S2

Male. Similar to female, vertex and dorsal mesosoma with brown-black coloration. Flagellomeres slightly longer than in females, 12th flagellomere elongate. Wing venation darker than in female.

Host plant. Ficus obtusifolia Kunth.

***Anidarnes globiceps* (Mayr, 1906)**
(Figs 2E, 3E, 4E, 5E, 6E, 7E)

1906 Mayr, G., *Wiener Entomologische Zeitung* 25: 184–185. Description (F, M) (comb.: *Sycophila globiceps*)

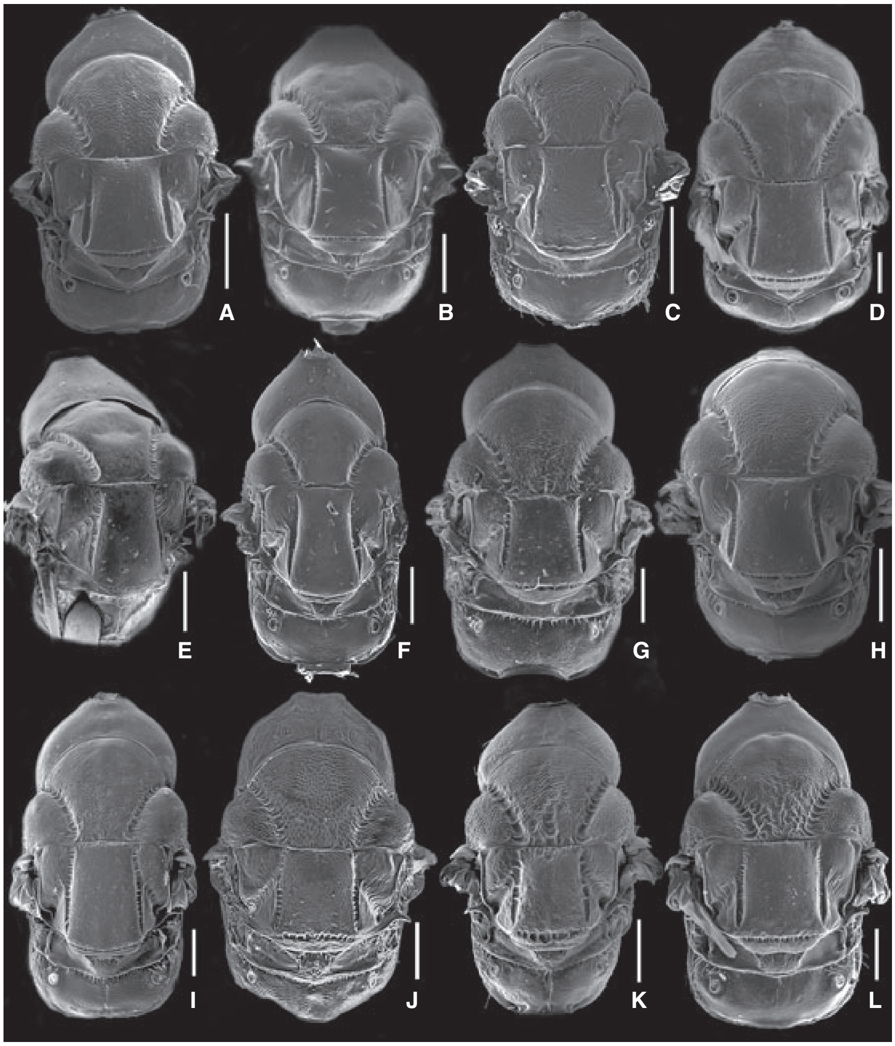

Fig. 6. Mesosoma of female *Anidarnes* species (SEM). (A) *A. bicolor* (Ashmead); (B) *A. brevicauda* Bouček; (C) *A. brevior* **sp.n.**; (D) *A. dissidens* **sp.n.**; (E) *A. globiceps* (Mayr); (F) *A. gracilis* **sp.n.**; (G) *A. isophlebiae* **sp.n.**; (H) *A. jimeneziae* **sp.n.**; (I) *A. longiscutellum* **sp.n.**; (J) *A. martinae* **sp.n.**; (K) *A. nigrus* **sp.n.**; (L) *A. rugosus* **sp.n.**. Scale = 200 μm.

1993 Bouček, Z., *Journal of Natural History* 27: 200. Combination (comb.: *Anidarnes globiceps*)

Type material. Lectotype ♀, Brazil, Santa Catarina, Blumenau (NMW, examined). Paralectotypes 1♀ 1♂ (NMW, examined).

Species re-description. See Appendix S1.

Host plant. *Ficus* sp.

Anidarnes gracilis **Farache & Rasplus sp.n.**
(Figs 2F, 3F, 4F, 5F, 6F, 7F)

Type material. Holotype ♀, Costa Rica, Pequena Helvetia, Hotel Los Heroes (10.474186°−84.830230°), 5.3.2008, ex. *F. trachelosyce*. n°JRAS2171_01, W. Ramirez & JY Rasplus leg. (CBGP). Paratypes : 8♀ 12♂, same data (5♀ 19♂ CBGP, 1♀ 1♂ BMNH, 1♀ 1♂ SAMC, 1♀ 1♂ MZSP).

Etymology. The specific name refers to the elongated mesosoma of the species.

Diagnosis. Predominantly yellow orange. Hind coxa darker than fore coxa. Metasoma dorsally brown-black. Malar sulcus present (Fig. 2F). Mesoscutellum 1.8–2× as long as wide, with smooth sculpture. Metascutellum present, transverse. Lateral ocellus closer to eye margin than to median ocellus. Propodeal median sulcus absent. Postmarginal vein present, but short (Fig. 7F). Malar depression clearly emarginate near malar sulcus (Fig. 2F). Ovipositor with median constriction, as long as 1.4× hind tibia.

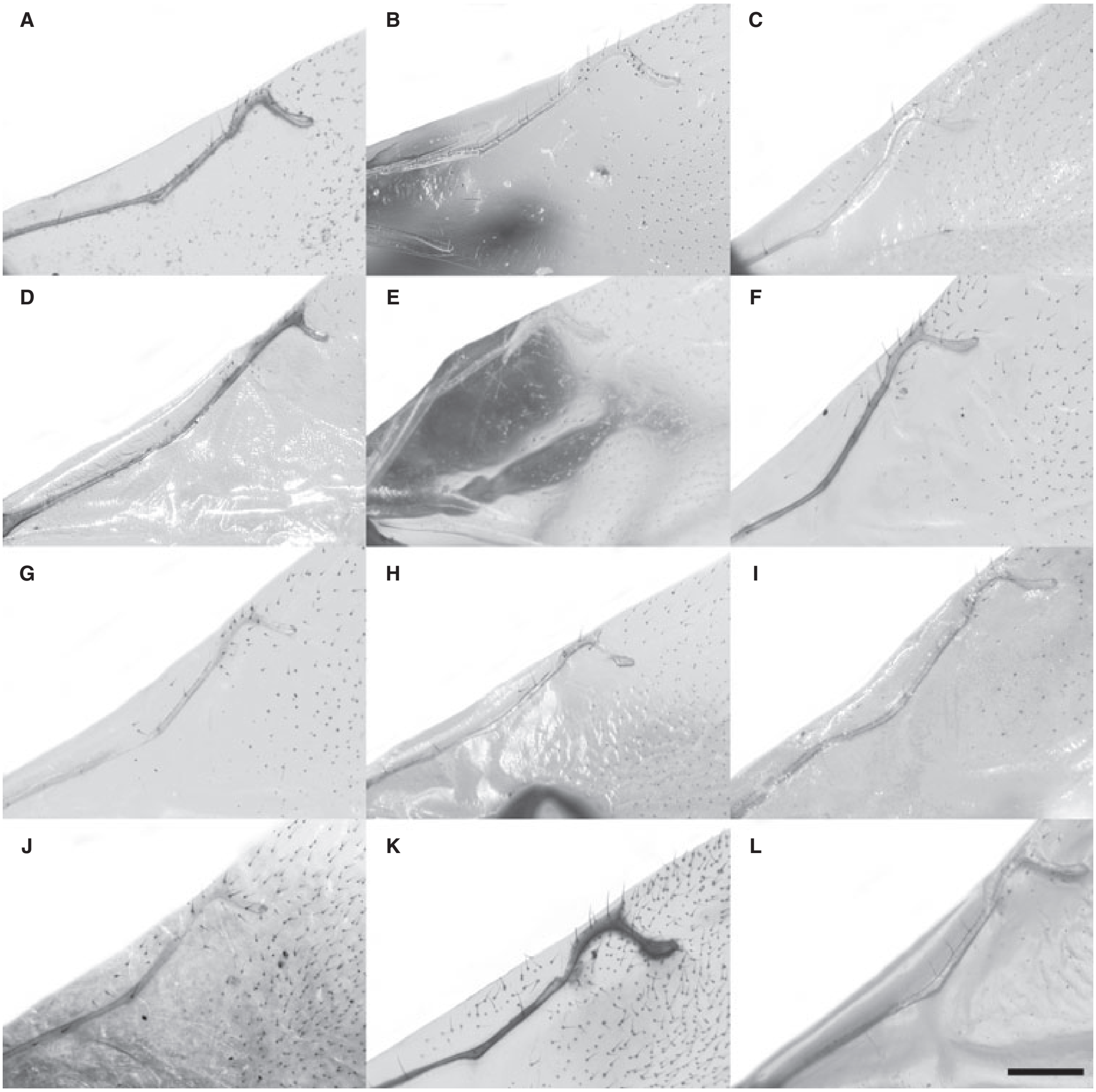

Fig. 7. Wing venation of female *Anidarnes* species. (A) *A. bicolor* (Ashmead); (B) *A. brevicauda* Bouček; (C) *A. brevior* **sp.n.**; (D) *A. dissidens* **sp.n.**; (E) *A. globiceps* (Mayr); (F) *A. gracilis* **sp.n.**; (G) *A. isophlebiae* **sp.n.**; (H) *A. jimeneziae* **sp.n.**; (I) *A. longiscutellum* **sp.n.**; (J) *A. martinae* **sp.n.**; (K) *A. nigrus* **sp.n.**; (L) *A. rugosus* **sp.n.**. Scale = 200 μm.

Female. Body length 2.6–2.7 mm. Ovipositor length 0.4–0.5 mm. Predominantly yellow orange. Scape yellow. Pedicel yellow orange. Funicle yellow orange to brown. Vertex slightly brown around ocelli. Pronotum yellow. Mesepisternum and metanotum smoky orange or brown. Legs yellow orange, coxae and trochanters yellow brown. Wings hyaline. Metasoma dorsally brown-black.

Head. Face smooth, shiny, with very faint reticulation. Pilosity short and sparse. Clypeus 1.4× as broad as high. Malar sulcus present. Epistomal groove shallow. Supraclypeal area broad, wider than 0.5× torulus diameter, predominantly smooth. Subantennal groove shallow and smooth. Interantennal projection lanceolate and short, exceeding the torulus by less than 1× torulus diameter. Distance from torulus to median ocellus 0.3–0.4× distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.6× pedicel length. Funicle with two anelli. First funicular segment 0.7× as long as wide. 12th flagellomere quadrate. POL 3.3× OOL. Vertex slightly concave. Median groove on vertex conspicuous.

Mesosoma. Mesoscutum smooth. Notauli densely crenulate. Mesoscutal lateral lobe reticulate, becoming smooth near notaulus. Mesoscutellum 1.8–2× as long as wide, with smooth sculpture. Frenal sulcus smooth. Frenum length *c*. 0.4× metascutellum length. Metascutellum trapezoidal, striate, without basal crenulation. Propodeal median line absent. Propodeal spiracle separated from the hind margin of metanotum by less than its own diameter. Wings with short and sparse pilosity. Postmarginal vein present, but short.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 1.4× hind tibia length.

Relative measurements. See Appendix S2.

Male. Similar to females, flagellomeres slightly longer than in females. Wings with long and dense pilosity.

Host plant. *Ficus trachelosyce* Dugand.

***Anidarnes isophlebiae* Farache & Rasplus sp.n.**
(Figs 2G, 3G, 4G, 5G, 6G, 7G)

Type material. Holotype ♀, Costa Rica, Puerto Viejo de Talamanca (9.637585°−82.708600°), 14.4.2010, ex *F. isophlebia*, n°JRAS2824_02, A. Cruaud & J.Y. Rasplus leg. (CBGP). Paratypes: 58♀ 23♂ same data (54♀ 19♂ CBGP, 1♀ 1♂ BMNH, 1♀ 1♂ SAMC, 2♀ 2♂ MZSP); 2♀ 1♂, Costa Rica, 12 km SW Bribri (9.559778°−82.9135°), 14.4.2010, ex *F. isophlebia*, n°JRAS2829_01 AC & JYR leg. (CBGP).

Etymology. The specific name refers to the host figs.

Diagnosis. Predominantly yellow orange. Metasoma lateroventrally yellow orange, dorsally dark brown. Interantennal projection long, exceeding the torulus by more than one torulus diameter (Fig. 3G). Metascutellum rectangular (Fig. 6G). Supraclypeal area reticulate (Fig. 3G). Propodeal spiracle clearly separated from metanotum (Fig. 6G). Ovipositor with median constriction, 1.5× as long as hind tibia.

Female. Body length 2.9–3.5 mm. Ovipositor length 1–1.1 mm. Predominantly yellow orange. Scape yellow, dorsal margin brown. Pedicel and funicle brown. Supraclypeal area and clypeus yellow. Vertex brown black. Pronotum more yellow. Posterior part of mesosoma slightly brown. Frenum dark brown. Legs yellow brown. Tarsi and foretibia yellow. Wings hyaline. Metasoma dorsally brown black.

Head. Face reticulate. Pilosity short and sparse. Clypeus 1.9× as broad as high. Malar sulcus absent. Epistomal groove shallow. Supraclypeal area broad, wider than 0.5× torulus diameter, reticulate. Subantennal groove shallow and crenulated. Interantennal projection lanceolate and long, exceeding the torulus by 1× torulus diameter. Distance from torulus to median ocellus 0.3× distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.9× pedicel length. Funicle with two anelli. First funicular segment 0.7× as long as wide. 12th flagellomere quadrate. POL 3.7× OOL. Vertex slightly concave. Median groove on vertex conspicuous.

Mesosoma. Anterior half of mesoscutum reticulated. Posterior half of mesoscutum rugose. Notauli sparsely crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.3× as long as wide, with engraved sculpture. Frenal sulcus densely crenulate. Frenum as long as metascutellum. Metascutellum rectangular, reticulate, without basal crenulation. Propodeal median line present as an impressed line. Propodeal spiracle separated from the hind margin of metanotum by about its own diameter. Wings with short and sparse pilosity. Postmarginal vein absent.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 1.5× hind tibia length.

Relative measurements. See Appendix S2

Male. Similar to females, wing pilosity longer and denser than in females.

Host plant. *Ficus isophlebia* Standley.

***Anidarnes jimeneziae* Farache & Rasplus sp.n.**
(Figs 2H, 3H, 4H, 5H, 6H, 7H)

Type material. Holotype ♀, Costa Rica, Santo Domingo de Heredia (9.988886°−84.083926°), 2.3.2008, ex. *F. jimenezii* n°JRAS2181, P. Hanson & J.Y. Rasplus leg. (CBGP). Paratypes: 4♂, same data (2♂ CBGP, 1♂ BMNH, 1♂ SAMC).

Etymology. The specific name refers to the host figs.

Diagnosis. Predominantly brown yellow. Pronotum yellow. Metasoma dorsally dark brown or black. Face with short and sparse pilosity (Fig. 5H). Interantennal projection short, exceeding the torulus by less than one torulus diameter. First funicular segment 0.7–0.9× as long as wide. Frenum reticulated. Notauli, axillular and frenal grooves smooth or shallowly crenulated. Propodeal median line present. Ovipositor with median constriction, as long as 1× hind tibia length.

Female. Body length 2 mm. Ovipositor length 0.5 mm. Predominantly brown yellow. Scape yellow, apically yellow brown. Pedicel brown. Funicle dark brown. Vertex brown or dark brown. Pronotum yellow. Frenum dark brown. Tibiae basally yellow brown and apically yellow. Tarsi yellow. Wings hyaline. Metasoma dorsally dark brown or black.

Head. Face reticulate. Pilosity short and sparse. Clypeus 1.7× as broad as high. Malar sulcus absent. Epistomal groove shallow. Supraclypeal area broad, wider than 0.5× torulus diameter, predominantly smooth. Subantennal groove shallow and smooth. Interantennal projection triangular, slightly lanceolate and short, exceeding the torulus by less than 1× torulus diameter. Distance from torulus to median ocellus 0.2× distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.6× pedicel length. Funicle with two anelli. First funicular segment 0.7× as long as wide. 12th flagellomere quadrate. POL 4.2× OOL. Vertex slightly concave. Median groove on vertex conspicuous.

Mesosoma. Anterior half of mesoscutum smooth, posterior half reticulated. Notauli sparsely crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.2× as long as wide, with engraved sculpture. Frenal sulcus faintly crenulate. Frenum length *c*. 0.7× metascutellum length. Metascutellum trapezoidal, striate, with a small median apical projection, without basal crenulation. Propodeal median line present as an impressed line. Propodeal spiracle separated from the hind margin of metanotum by less than its own diameter. Wings with short and sparse pilosity. Postmarginal vein present, but short.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 1× hind tibia length.

Relative measurements. See Appendix S2.

Male. Body slightly darker than female. Flagellomeres slightly longer and less compressed. 12th flagellomere elongate.

Host plant. Ficus jimenezii Standley.

***Anidarnes longiscutellum* Farache & Rasplus sp.n.**
(Figs 2I, 3I, 4I, 5I, 6I, 7I)

Type material. Holotype ♀, Brazil, São Paulo, Ribeirão Preto (−21.198135°−47.900451°), 6.8.2008, ex. *F. eximia*, n°168-1, LMR Teixeira & al. leg. (CBGP). Paratypes: 5♀ 1♂, same data (2♀ 1♂ CBGP, 1♀ BMNH, 1♀ SAMC, 1♀ MZSP). 2♀, Brazil, São Paulo, Ribeirão Preto (−21.197201°−47.892800°), 6.9.2009, ex. *F. eximia*, n° 158, FHAF & LMRT leg. (CBGP).

Etymology. The specific name refers to the long mesoscutellum and the relatively long mesosoma exhibited by this species.

Diagnosis. Predominantly yellow orange. Metasoma dorsally dark brown to black. Propodeal median line present, crenulate (Fig. 6I). Postmarginal vein absent (Fig. 7I). Fore and hind coxae with the same coloration. Malar depression shallowly emarginate near malar sulcus (Fig. 2I). Ovipositor with median constriction, as long as 1.1× hind tibia.

Female. Body length 2.3–3.3 mm. Ovipositor length 0.6 mm. Predominantly yellow orange. Scape and pedicel yellow. Funicle yellow brown. Vertex dark brown. Mesepimeron slightly brown. Tibiae and tarsi yellow. Wings hyaline. Metasoma dorsally dark brown to black.

Head. Face shallowly reticulate. Pilosity short and sparse. Clypeus as broad as high. Malar sulcus present. Epistomal groove absent. Supraclypeal area narrow, width smaller than 0.3× torulus diameter, faintly reticulate. Subantennal groove shallow and crenulated. Interantennal projection lanceolate and long, exceeding the torulus by 1× torulus diameter. Distance from torulus to median ocellus 0.3× distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.6× pedicel length. Funicle with two anelli. First funicular segment 0.9–1× as long as wide. 12th flagellomere elongate. POL 2.6× OOL. Vertex slightly concave. Median groove on vertex conspicuous.

Mesosoma. Mesoscutum reticulated. Notauli densely crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.6–1.7× as long as wide. With engraved sculpture. Frenal sulcus faintly crenulate. Frenum length *c*. 0.2× metascutellum length. Metascutellum trapezoidal, reticulate, with a basal crenulation. Propodeal median line present as a crenulated furrow. Propodeal spiracle separated from the hind margin of metanotum by less than its own diameter. Wings with short and sparse pilosity. Postmarginal vein absent.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 1.1× hind tibia length.

Relative measurements. See Appendix S2.

Male. Similar to females, body predominantly brown to smoky yellow. Wings with long and dense pilosity.

Host plant. Ficus eximia Schott.

***Anidarnes martinae* Farache & Rasplus sp.n.**
(Figs 2J, 3J, 4J, 5J, 6J, 7J)

Type material. Holotype ♀, U.S.A., Florida Florida City (25.420393°−80.534593°), 29.4.2010, ex *F. aurea* n° JRAS 2871-03, A. Cruaud & JY Rasplus leg. (CBGP). Paratypes: 2♀ 2♂, same data ; 3♂, U.S.A., Florida, Miami University Campus (25.72°−80.28°), 9.1994, ex *F. aurea* n° JRAS1155, M. Hossaert-McKey leg (2♂) (CBGP).

Etymology. The specific name is dedicated to our friend and colleague Martine Hossaert-McKey who first collected this species in Miami.

Diagnosis. Predominantly dark brown. Head with strong metallic luster, green, slightly red near torulus, with a transversal blue stripe beginning after posterior ocelli and fading before occipital foramen. Pronotum yellow. Mesoscutellum and lateral lobe of mesoscutum slightly yellow. Wings hyaline. Antenna with one annellus (seven funicular segments bearing sensillae). Ovipositor with median constriction, as long as 0.3× hind tibia length.

Female. Body length 2.65 mm. Ovipositor length 0.3 mm. Predominantly dark brown. Scape yellow, brown in the apical margin. Pedicel and funicle brown. Tarsi and foretibia yellow. Head with strong metallic luster, green, slightly red near torulus, with a transversal blue stripe beginning after posterior ocelli and fading before occipital foramen. Pronotum yellow. Mesoscutellum and lateral lobe of mesoscutum slightly yellow. Wings hyaline.

Head. Face reticulate. Pilosity short and sparse. Clypeus 2.4× as broad as high. Malar sulcus absent. Epistomal groove present, delimiting clypeus dorsally. Supraclypeal area broad, wider than 0.5× torulus diameter, predominantly smooth. Subantennal groove shallow and smooth. Interantennal projection triangular and short, exceeding the torulus by less than 1× torulus diameter. Distance from torulus to median ocellus 0.3× distance from torulus to oral margin. Distance between toruli equal to torulus diameter. Scape length 2.9× pedicel length. Funicle with one anelli. First funicular segment 0.7× as long as wide. 12th flagellomere elongate. POL 3.9× OOL. Vertex slightly concave. Median groove on vertex absent.

Mesosoma. Anterior half of mesoscutum reticulated. Posterior half of mesoscutum engraved. Notauli densely crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.3× as long as wide. With faintly engraved sculpture. Frenal sulcus densely crenulate. Frenum length *c*. 0.7× metascutellum length. Metascutellum trapezoidal, medially reticulate, laterally striate and without basal crenulation. Propodeal median line present as an impressed line. Propodeal spiracle separated from the hind margin of metanotum by less than its own diameter. Wings with short but dense pilosity. Postmarginal vein absent.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 0.3× hind tibia length.

Relative measurements. See Appendix S2.

Male. Similar to females, lateral lobe of mesoscutum and mesoscutellum yellow lighter than the female. Wings with long and dense pilosity.

Host plant. *Ficus aurea* Nuttal.

Anidarnes niger **Farache & Rasplus sp.n.**
(Figs 2K, 3K, 4K, 5K, 6K, 7K)

Type material. Holotype ♀, Colombia, Cundinamarca, Bogotá D.C., Ciudad Universitaria (4.638568°−74.089985°), 16.6.2009, ex *F. andicola*, n°JRAS2957, S Jansen G leg. (CBGP). Paratypes 17♀ 21♂ (14♀ 18♂ CBGP, 1♀ 1♂ BMNH, 1♀ 1♂ SAMC, 1♀ 1♂ MZSP), same data.

Etymology. The specific name refers to black coloration of the body.

Diagnosis. Body black. Wings hyaline, with slightly infuscate median region. Mesoscutum bearing strong crenulations along the transcutal line. Frenal sulcus wider than frenum and coarsely crenulated (Fig. 6K). Wings with long and dense pilosity. Propodeum with median striae (Fig. 7K). Ovipositor with median constriction, 1.2× as long as hind tibia.

Female. Body length 2–2.1 mm. Ovipositor length 0.5–0.6 mm. Predominantly black. Scape and pedicel yellow. Funicle yellow brown. Coxae black-brown. Femora brown. Tibiae yellow brown. Tarsi yellow. Wings hyaline, with slightly infuscate median region.

Head. Face reticulate. Pilosity long and conspicuous. Clypeus 1.5× as broad as high. Malar sulcus absent. Epistomal groove present, delimiting clypeus dorsally. Supraclypeal area narrow, width smaller than 0.3× torulus diameter, Faintly reticulate. Subantennal groove shallow and crenulated. Interantennal projection triangular and short, exceeding the torulus by less than 1× torulus diameter. Distance from torulus to median ocellus 0.3–0.4× distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 1.9–2.3× pedicel length. Funicle with two anelli. First funicular segment 0.8–0.9× as long as wide. 12th flagellomere quadrate. POL 3.9× OOL. Vertex slightly concave. Median groove on vertex shallow, conspicuous near occipital foramen.

Mesosoma. Anterior half of mesoscutum reticulated. Posterior half of mesoscutum rugose. Notauli sparsely crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.5× as long as wide. With coarsely engraved sculpture. Frenal sulcus sparsely crenulate. Frenum length *c*. 0.6× metascutellum length. Metascutellum trapezoidal, reticulate, without basal crenulation. Propodeal median line present as longitudinal striae. Propodeal spiracle separated from the hind margin of metanotum by less than its own diameter. Wings with long and dense pilosity. Postmarginal vein present, but short.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 1.2× hind tibia length.

Relative measurements. See Appendix S2.

Male. Similar to females, flagellomeres slightly longer than in females.

Host plant. *Ficus americana andicola* Standley.

Anidarnes rugosus **Farache & Rasplus sp.n.**
(Figs 2L, 3L, 4L, 5L, 6L, 7L)

Type material. Holotype ♀, Brazil, São Paulo, Teodoro Sampaio (−22.36578°−52.314398°), 3.5.2008, ex *F. crocata* n°47-10, LMR Teixeira leg. (CBGP). Paratypes: 11♀ 3♂ (8♀ 1♂ CBGP, 1♀ 1♂ BMNH, 1♀ 1♂ SAMC, 1♀ MZSP), same data.

Etymology. The specific name refers to the rugose sculpture observed on the mesoscutum of this species.

Diagnosis. Predominantly dark brown. Head yellow brown, vertex dark brown. Pronotum yellow. Mesoscutum posteriorly rugose. Mesoscutellum rectangular, with parallel lateral sides. Interantennal projection long, keel like, exceeding the torulus by one torulus diameter. 12th antennal flagellomere elongate. Notauli, axillular and frenal grooves conspiscuously and densely crenulated. First funicular segment transverse, 0.4–0.6× as long as wide. Ovipositor with median constriction, 0.8× as long as hind tibia.

Female. Body length 2.6–2.7 mm. Ovipositor length 0.4–0.5 mm. Predominantly dark brown. Scape yellow, dorsally brown especially in distal margin. Pedicel and funicle brown. Head yellow brown, vertex dark brown. Pronotum yellow.Tarsi yellow. Wings hyaline.

Head. Face reticulate. Pilosity long and conspicuous. Clypeus 1.9× as broad as high. Malar sulcus absent. Epistomal groove shallow. Supraclypeal area broad, wider than 0.5×torulus diameter, faintly reticulate. Subantennal groove shallow and smooth. Interantennal projection lanceolate and long, exceeding the torulus by 1× torulus diameter. Distance from torulus to median ocellus 0.4–0.5× distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.5–3.1× pedicel length. Funicle with two anelli. First funicular segment 0.4–0.6× as long as wide. 12th flagellomere elongate. POL 2.9–3.8× OOL. Vertex slightly concave. Median groove on vertex absent.

Mesosoma. Anterior half of mesoscutum smooth, posterior half rugose. Notauli densely crenulate. Mesoscutal lateral lobe homogeneously reticulate. Mesoscutellum 1.3–1.4× as long as wide, with engraved sculpture. Frenal sulcus densely crenulate. Frenum length *c.* 0.7× metascutellum length. Metascutellum trapezoidal, reticulate, without basal crenulation. Propodeal median line absent. Propodeal spiracle separated from the hind margin of metanotum by about its own diameter. Wings with short and sparse pilosity. Postmarginal vein absent.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 0.8× hind tibia length.

Relative measurements. See Appendix S2.

Male. Similar to females, wings with long and dense pilosity.

Host plant. *Ficus crocata* (Miquel) Miquel.

Key to species of *Anidarnes* Bouček

1 Ovipositor without median constriction and depigmentation (Fig. 2D). Interantennal process flat, longer than 2× torulus diameter (Fig. 3D). Metascutellum triangular (Fig. 1B). Hypopygium apex (mucro) long and narrow (Fig. 2D). *F. obtusifolia* .... ***A. dissidens* sp.n.**
– Ovipositor with median constriction and depigmentation (Fig. 2A). Interantennal process triangular or lanceolate. Metascutellum rectangular or trapezoidal. Mucro short and broad **2**
2(1) Head metallic (Figs 2J, 5J), body yellowish to brown. Antenna with one annellus (seven funicular segments bearing sensillae) (Fig. 3J). *F. aurea* .... ***A. martinae* sp.n.**
– Absence of metallic tinge on the head. Antenna with two annelli (six funicular segments bearing sensillae) **3**
3(2) Malar sulcus present (Fig. 2E, F) **4**
– Malar sulcus absent **6**
4(3) Metascutellum unconspicuous, poorly delimitated (Figs 5E, 6E). Ovipositor sheaths as long as hind tibia. OOL as long as OL (Fig. 5E). *Ficus sp.* .... ***A. globiceps* (Mayr)**
– Metascutellum present, transverse. Ovipositor sheaths longer than hind tibia. Lateral ocellus closer to eye margin than to median ocellus **5**
5(4) Propodeal median line present, crenulate (Fig. 6I). Postmarginal vein absent (Fig. 7I). Fore and hind coxae with the same coloration. Malar depression shallowly emarginate near malar sulcus (Fig. 2I). *F. eximia* .... ***A. longiscutellum* sp.n.**
– Propodeal median sulcus absent. Postmarginal vein present, but short (Fig. 7F). Hind coxa darker than fore coxa. Malar depression clearly emarginate near malar sulcus (Fig. 2F). *F. trachelosyce* .... ***A. gracilis* sp.n.**
6(3) Body black (Fig. 5K). Wings with long and dense pilosity, infuscated on the disc. Propodeum with median striae (Fig. 7K). Mesoscutum bearing strong crenulations along the transcutal line. Frenal sulcus wider than frenum and coarsely crenulated (Fig. 6K). *F. andicola* .... ***A. niger* sp.n.**
– Body yellow to brown, never homogeneously black. Wing pilosity short and sparse. Other characters different **7**

7(6) Ovipositor longer than hind tibia. Anterior half of mesoscutum mostly reticulated (Fig. 6A, G) **8**
– Ovipositor as long as or shorter than hind tibia. Anterior half of mesoscutum mostly smooth (Fig. 6B, L) **9**
8(7) Metascutellum trapezoidal (Fig. 6A), with a small median tooth on posterior margin. Propodeal spiracle contiguous to metanotum (Fig. 6A). Supraclypeal area mostly smooth (Fig. 3A). Interantennal projection short, exceeding the torulus by less than one torulus diameter (Fig. 3A). Metasoma entirely brown-black. *F. aurea* .... ***A. bicolor*** **(Ashmead)**
– Metascutellum rectangular (Fig. 6G). Propodeal spiracle clearly separated from metanotum (Fig. 6G). Supraclypeal area reticulate (Fig. 3G). Interantennal projection long, exceeding the torulus by more than one torulus diameter (Fig. 3G). Metasoma lateroventrally yellow orange, dorsally dark brown. *F. isophlebia* .... ***A. isophlebiae*** **sp.n.**
9(7) Scutellum and anterior half of mesonotum smooth (Fig. 5B). Mesoscutum lateral lobe reticulate, becoming smooth near notaulus (Fig. 6B). *F. costaricana* .... ***A. brevicauda*** **sp.n.**
– Scutellum not smooth, engraved. Mesoscutum lateral lobe with homogeneous reticulation **10**
10(9) Mesoscutum posteriorly rugose. Mesoscutellum rectangular, with parallel lateral sides. Interantennal projection long, keel like, exceeding the torulus by one torulus diameter. 12th antennal flagellomere elongate. Notauli, axillular and frenal grooves conspicuously and densely crenulated. First funicular segment transverse, 0.4–0.6× as long as wide. *F. crocata* ... . ***A. rugosus*** **sp.n.**
– Mesoscutum posteriorly engraved, without any rugae. Mesoscutellum trapezoidal, the lateral sides diverging posteriorly. Interantennal projection short, not exceeding the torulus by one torulus diameter. Notauli, axillular and frenal grooves smooth or shallowly crenulated. First funicular segment 0.7–0.9× as long as wide **11**
11(10) Propodeal median line present. Face with short and sparse pilosity (Fig. 5H). Frenum reticulated. *F. jimenezii* .. .. ***A. jimeneziae*** **sp.n.**
– Propodeal median line absent. Face with long and dense pilosity (Fig. 5C). Frenum smooth *F. americana* .... ***A. brevior*** **sp.n.**

Sequence data

The final matrix contained ten ingroup species and four outgroups, represented by 23 individuals and 3937 bp (*COI*+*Cytb* = 2205 bp, *EF-1α* = 517 bp, 28S rRNA = 1215 bp). Of these, 1210 bp were variable and 744 bp were parsimony informative. Alignment of protein coding genes revealed no stop codons or frame shifts. Models chosen by MrAIC for each partition were GTR + I + Γ (mtDNA), GTR + Γ (28S rRNA) and K2P + Γ (*EF-1α*). As RAxML does not implement the K2P model, we used GTR instead. Given that α and the proportion of invariable sites can not be optimised independently from each other (Gu, 1995) and following Stamatakis' recommendations (RAxML manual), we used GTR + Γ with four discrete rate categories for all partitions.

Phylogenetic analyses

The trees reconstructed using ML and Bayesian methods showed the same topology (Fig. 8). Parsimony-based analysis produced a single most parsimonious (MP) tree of 2238 steps (CI = 0.674, RI = 0.653), with a slightly different topology (Fig. 9). Recovered ML and Bayesian phylogenies supported monophyly of *Anidarnes*, and *A. dissidens* was recovered sister to all other *Anidarnes* species with strong support (BP_{ML} = 96, PP = 1.00) To the contrary, the undescribed genus rendered *Anidarnes* paraphyletic in the most parsimonious tree.

Anidarnes martinae and *A. rugosus* formed a grade of species (not resolved in MP analysis) basal to a well-supported clade (BP_{MP} = 74, BP_{ML} = 98, PP = 1.00) grouping all remaining *Anidarnes* species. In this latter clade, phylogenetic relationships were only partly resolved. *Anidarnes bicolor* and *A. jimeneziae* were always recovered as sister taxa with strong support values (BP_{MP} = 100, BP_{ML} = 100, PP = 1.00). *Anidarnes gracilis* and *A. longiscutellum* formed a strong monophyletic group (BP_{MP} = 99, BP_{ML} = 100, PP = 1.00) and *A. brevior* and *A. niger* were sister species with moderate to strong supports (BP_{MP} = 67, BP_{ML} = 98, PP = 1.00). A moderately supported clade grouping *A. niger, A. brevior, A. gracilis* and *A. longiscutellum* was recovered by ML and Bayesian analyses only (BP = 60, PP = 0.98).

Discussion

The monophyly of *Anidarnes* in its present delimitation is not always supported by our molecular phylogenetic analyses. *Anidarnes dissidens* does not cluster with other *Anidarnes* in the most parsimonious tree and is sister to the remaining *Anidarnes* species in both ML and Bayesian trees. Morphologically, *A. dissidens* exhibits several characters that are not recovered in other *Anidarnes* species. The marginal vein is longer than the stigmal (Fig. 7D) and the interantennal projection is large (Fig. 3D). Furthermore, *A. dissidens* does not exhibit the characteristic ovipositor of other *Anidarnes* species. In these species, the ovipositor sheaths are generally strongly bent downward medially with a break highlighted by an unpigmented area (Fig. 2A, F, H), and the hypopygial mucro is short. By contrast, in *A. dissidens,* the ovipositor has no medial constriction and depigmentation (Fig. 2D), and the mucro is long.

This combination of characters strongly suggests that *A. dissidens* may deserve generic status. However, we believe additional taxonomic sampling is necessary before establishing a new monotypic genus, and therefore keep *A. dissidens* in *Anidarnes*. Consequently, for the time being, no single apomorphies define *Anidarnes*, and a combination of characters is needed to define the genus.

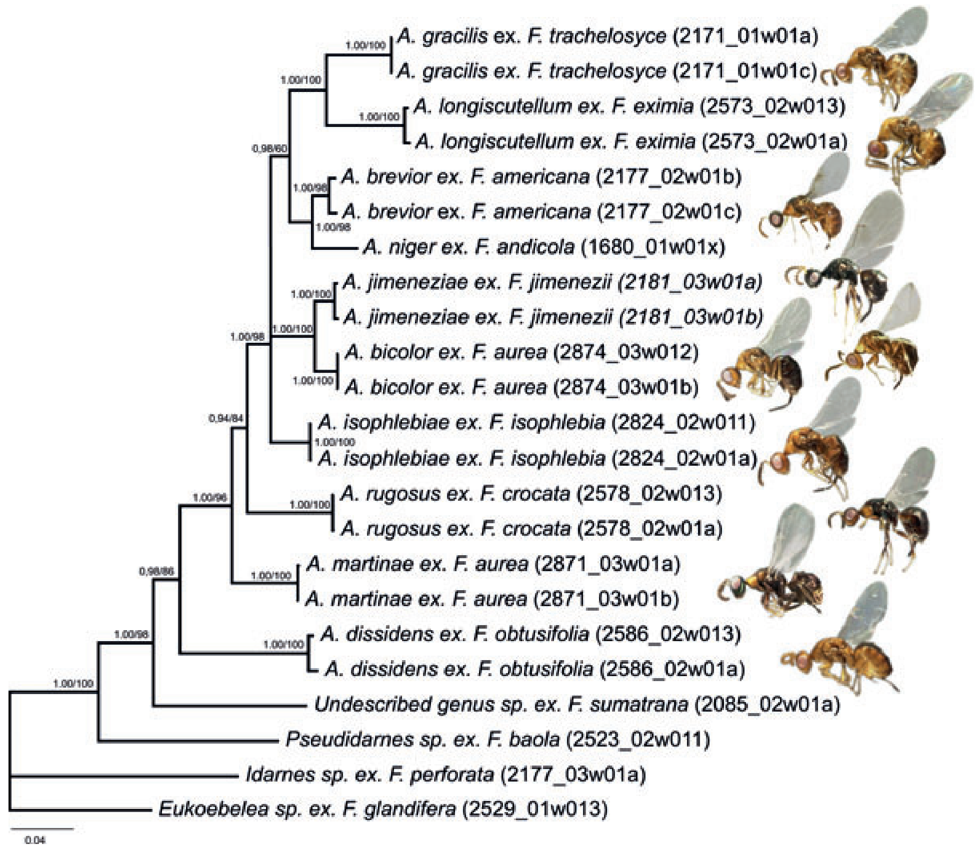

Fig. 8. Phylogram of relationships among *Anidarnes* species and four outgroup taxa. Likelihood bootstrap values (BP_{ML}) and Bayesian posterior probabilities (PP) are indicated at nodes. Nodes with $BP_{ML} < 65$ and $PP < 0.90$ are collapsed.

All analyses strongly support species without a median groove on the vertex (*A. dissidens, A. martinae* and *A. rugosus*) as the earliest-branching lineages of extant species in the genus. Within the group of *Anidarnes* with 'broken' ovipositor sheaths, *A. martinae,* which is resolved as sister to the remaining species (excluding *A. dissidens*) in the ML and Bayesian trees, exhibits the most divergent morphological characters. *Anidarnes martinae* is the only *Anidarnes* species with metallic tinge (the head is metallic blue). Within the *Pseudidarnes* + (undescribed genus + *Anidarnes*) clade of Sycophaginae, metallic tinge is reminiscent of *Pseudidarnes* (mostly metallic) and is also present in all species of the undescribed genus known to us (ten spp.). *Anidarnes martinae* also exhibits a unique structure of the flagellum (Fig. 3G), where a single annellus is present. Furthermore, the second funicular segment is not anneliform and bears multiporous plate sensillae.

Our molecular phylogenetic analyses show strong support for a clade grouping all *Anidarnes* species with a median occipital groove (*A. gracilis*, *A. longiscutellum, A. niger, A. brevior, A. bicolor*, *A. jimeneziae* and *A. isophlebiae*). However, relationships among these species remain partly unresolved, which may reflect rapid branching events leading to three or four descendant lineages.

Both probabilistic and parsimony methods recover *A. gracilis* and *A. longiscutellum* as sister taxa. This result is consistent with our morphological observations. Indeed, several morphological characters are shared by these species (presence of malar sulcus, head and mesosoma predominantly smooth, body colour mainly yellow). These characters are also shared with *A. globiceps*, which may indicate a close relationship between the three species.

Anidarnes bicolor and *A. jimeneziae,* which are morphologically related, are also strongly supported as sister taxa. Interestingly, their host figs (*F. aurea* and *F. jimenezii* respectively) belong to the *Ficus aurea* complex in the last morphological analysis (Berg, 2007) and were recently considered as synonyms (Berg, 2009). It is noteworthy that despite rather distinctive fig and leaf characters, *F. isophlebia* is also included in the *F. aurea* complex (Berg, 2007). However, *A. isophlebiae* does not appear closely related (both morphologically and molecularly) to *A. bicolor* and *A. jimeneziae,* and may represent an independent colonisation of the *F. aurea* aggregate by *Anidarnes*. In the same manner, *A. brevior* and *A. niger* are always recovered as sister taxa whith strong support. These species are associated with figs of the *F. americana* complex (Berg, 2007). *Ficus americana* and *F. andicola* are considered subspecies within the *F. americana* aggregate but

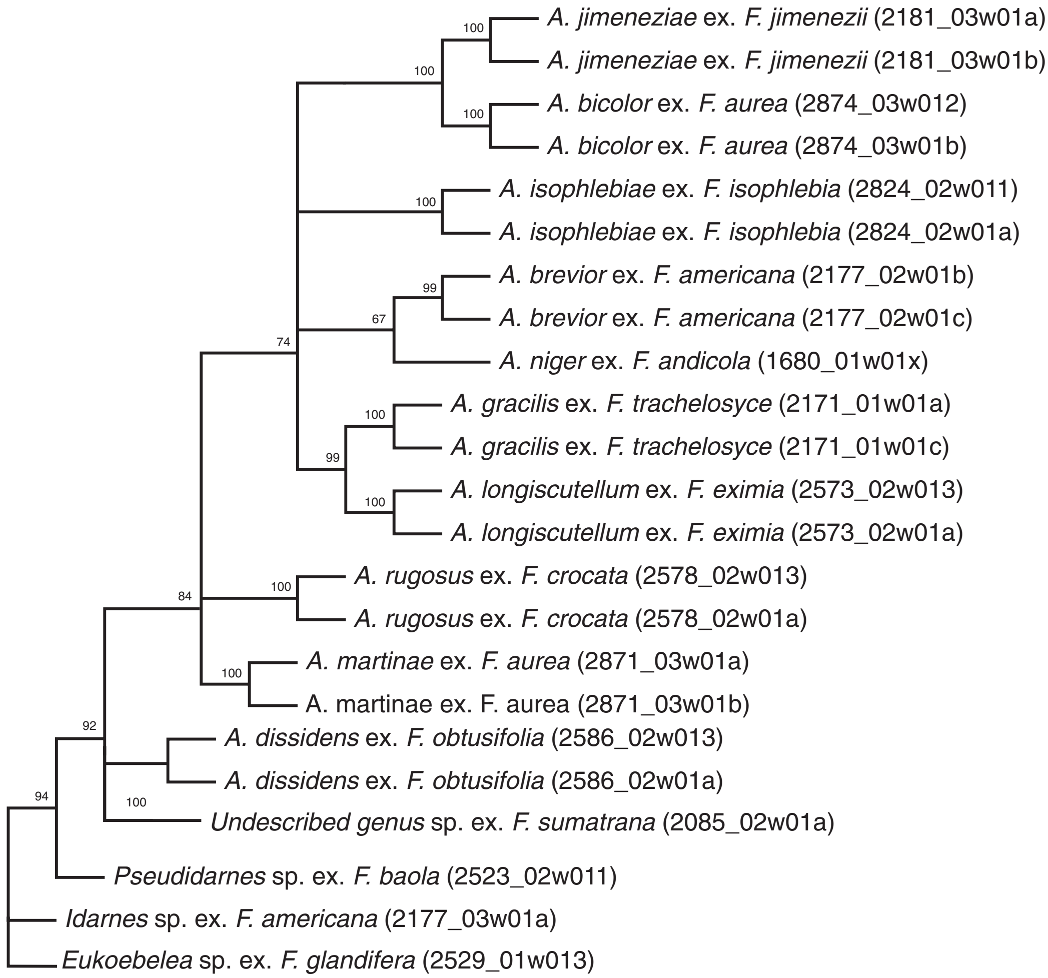

Fig. 9. Cladogram of relationships among *Anidarnes* species and four outgroup taxa. Parsimony bootstrap values (BP_{MP}) are indicated at nodes. Nodes with $BP_{MP} < 65$ are collapsed.

exhibit characters that suggest they may deserve species status (Berg, 2007). In both cases, *Anidarnes* sister species are clearly differentiable based on morphology. Specifically, *A. niger* and *A. brevior* are morphologically quite divergent. *Anidarnes niger* is especially characterised by large wing surface, a character that could be related to the high altitude habitat of the Andean *F. andicola*: montane and submontane forest at altitudes between 1200 and 3000 m.

These observations suggest that *Anidarnes* may occasionally speciate on the host, without fig speciation (their hosts are still considered as subspecies but not species), a result already observed in several group of pollinators (Cook & Rasplus, 2003; Cruaud *et al.*, 2012) and also in nonpollinating fig wasps (Cruaud *et al.*, unpublished data). Sycophaginae generation time is much shorter than fig generation time, and this could explain such speciation by duplication. Divergence between species isolated on different populations (subspecies) of their host fig tree may also explain multiple closely-related wasp species associated with a single fig species (Cook & Segar, 2010). Finally, our results suggest that independent colonisations of the same *Ficus* host may occur. This is the case for *A. martinae* and *A. bicolor* that co-occur on *F. aurea* in Florida, but belong to two unrelated lineages.

This study is the first to thoroughly examine the morphology of a group of neotropical nonpollinating fig wasps. It lays the foundation for comparative studies of *Anidarnes* within a phylogenetic framework. Hopefully, this will encourage further research on taxonomy and phylogeny of fig wasps, which are key steps toward a better understanding of the evolution and functioning of their communities.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
10.1111/j.1365-3113.2012.00644.x

Appendix S1. *Anidarnes* Bouček, 1993. Species redescriptions and nontype materials.

Appendix S2. *Anidarnes* Bouček, 1993. Relative measurements.

Acknowledgements

We are very much indebted to A. Polaszek (BMNH, London, U.K.), N. Dale-Skey Papilloud (BMNH, London, U.K.), E. Grissell (USNM, Washington, U.S.A.) and D. Zimmermann (NMW, Vienna, Austria) for the loan of type material. We acknowledge P. Hanson and W. Ramirez for their kind help in Costa Rica. L.F.M. Coelho, L. P. Rocha, M. T. Cerezini, L.M.R. Teixeira and M.E. Lapate contributed to the specimen sampling in Brazil. S. Jansen-G contributed with specimens from Colombia. We wish to thank L. Soldati and Rodrigo Silva for help in SEM imaging. This study was supported by the French National Research Agency (ANR) grant that supports the 'NiceFigs' project and Sao Paulo Research Foundation (FAPESP) grant #04/10299-4 that supported RASP. Sequencing was supported by a Genoscope project (@-Speed-Id) managed by JYR. The Synthesys project. http://www.synthesys.info/ funded the stay of JYR at the NMW. FHAF was funded by FAPESP (#07/06054-4, #10/51158-5), PRPG-USP and PROAP. RASP was also funded by CNPq (#302769/2008-0).

Authors' contributions

RASP and JYR designed the research. All authors provided material or data. GG performed DNA sequencing. FHAF and JYR conducted morphological analyses. AC performed phylogenetic analyses. FHAF, AC and JYR wrote the manuscript with major comments from RASP. All authors read and approved the final manuscript.

References

Arnett, R.H., Samuelson, G.A. & Nishida, G.M. (1993) *The Insect and Spider Collections of the World*, 2nd edn. Sandhill Crane Press, Inc., Gainesville, FL.

Berg, C.C. (2007) Proposals for treating four species complexes in *Ficus* subgenus *Urostigma* section *Americanae* (Moraceae). *Blumea*, **52**, 295–312.

Berg, C.C. (2009) 27B. Moraceae (Ficus). *Flora of Ecuador*, Vol. 85 (ed. by G. Harling and C. Persson), pp. 1–148. Department of Plant and Environmental Sciences, University of Gothenburg, Göteborg.

Bouček, Z. (1988) *Australasian Chalcidoidea (Hymenoptera). A Biosystematic Revision of Genera of Fourteen Families, with a Reclassification of Species*. C.A.B. International, Wallingford.

Bouček, Z. (1993) The genera of chalcidoid wasps from *Ficus* fruit in the New World. *Journal of Natural History*, **27**, 173–217.

Bronstein, J.L. (1999) Natural history of *Anidarnes bicolor* (Hymenoptera: Agaonidae), a galler of the Florida strangling fig (*Ficus aurea*). *Florida Entomologist*, **82**, 454–461.

Cook, J.M. & Rasplus, J.-Y. (2003) Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology and Evolution*, **18**, 241–248.

Cook, J.M. & Segar, S.T. (2010) Speciation in fig wasps. *Ecological Entomology*, **35**, 54–66.

Cruaud, A., Jabbour-Zahab, R., Genson, G. *et al.* (2010) Laying the foundations for a new classification of Agaonidae (Hymenoptera: Chalcidoidea), a multilocus phylogenetic approach. *Cladistics*, **26**, 359–387.

Cruaud, A., Jabbour-Zahab, R., Genson, G. *et al.* (2011a) Out-of-Australia and back again: the worldwide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae). *Journal of Biogeography*, **38**, 209–225.

Cruaud, A., Jabbour-Zahab, R., Genson, G. *et al.* (2011b) Phylogeny and evolution of life-history strategies in the Sycophaginae non-pollinating fig wasps (Hymenoptera, Chalcidoidea). *BMC Evolutionary Biology*, **11**, 178.

Cruaud, A., Jabbour-Zahab, R., Genson, G., Ungricht, S. & Rasplus, J.-Y. (2012) Testing the emergence of New Caledonia: fig wasp mutualism as a case study and a review of evidence. *PLoS ONE*, **7**, e30941.

Drummond, A.J., Ashton, B., Cheung, M. *et al.* (2010) *Geneious v5.5.7* [WWW document]. URL http://www.geneious.com/ [accessed on 10 April 2012].

Gibson, G.A.P. (1997) Morphology and terminology. *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)*, Chapter 2 (ed. by G.A.P. Gibson, J.T. Huber and J.B. Woolley), pp. 16–44. National Research Council Research Press, Ottawa.

Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 1–13.

Gordh, G. (1975) The comparative external morphology and systematics of the Neotropical parasitic fig wasp *Idarnes* (Hymenoptera: Torymidae). *University of Kansas Science Bulletin*, **50**, 389–455.

Gu, X. (1995) Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. *Molecular Biology and Evolution*, **12**, 546–557.

Heraty, J.M. & Hawks, D. (1998) Hexamethyldisilazane: A chemical alternative for drying insects. *Entomological News*, **109**, 369–374.

Huelsenbeck, J.P. & Ronquist, F. (2001) MrBayes: Bayesian inferences of phylogeny. *Bioinformatics*, **17**, 754–755.

Janzen, D.H. (1979) How to be a fig. *Annual Review of Ecology and Systematics*, **10**, 13–51.

Katoh, K., Kuma, K., Toh, H. & Miyata, T. (2005) MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research*, **33**, 511–518.

Kerdelhué, C., Rossi, J.P. & Rasplus, J.Y. (2000) Comparative community ecology studies on Old World figs and fig wasps. *Ecology*, **81**, 2832–2849.

Marussich, W.A. & Machado, C.A. (2007) Host-specificity and coevolution among pollinating and nonpollinating New World fig wasps. *Molecular Ecology*, **16**, 1925–1946.

Mayr, G. (1885) Feigeninsecten. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, **35**, 147–250.

Nylander, J.A.A. (2004) *MrAIC.pl*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Upssala.

Rambaut, A. & Drummond, A.J. (2004) *Tracer v1.4.1* [WWW document]. URL http://tree.bio.ed.ac.uk/software/tracer/ [accessed on 10 April 2012].

Rasplus, J.Y., Kerdelhué, C., Le Clainche, I. & Mondor, G. (1998) Molecular phylogeny of fig waps (Hymenoptera). Agaonidae are not monophyletic. *Compte Rendu de l'Académie des Sciences de Paris*, **321**, 517–527.

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.

Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007) MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, **24**, 1596–1599.

Weiblen, G. (2002) How to be a fig wasp? *Annual Review of Entomology*, **47**, 299–330.

West, S.A. & Herre, E.A. (1994) The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. *Proceedings of the Royal Society B: Biological Sciences*, **258**, 67–72.

West, S.A., Herre, E.H., Windsor, D.M. & Green, R.S. (1996) The ecology and evolution of the New World non-pollinating fig wasp communities. *Journal of Biogeography*, **23**, 447–458.

Wiebes, J.T. (1966) Provisional host catalogue of fig wasps (Hymenoptera, Chalcidoidea). *Zoologische Verhandelingen*, **83**, 1–44.

Wiebes, J.T. (1995) The New World Agaoninae (pollinators of figs). *Verhandelingen der Koninklijke Nederlandsche (Nederlandse) Akademie van Wetenschappen*, **94**, 1–60.

Accepted 18 June 2012

Farache, F. H. A.; Cruaud, A; Genson, G. Pereira, R.A.S. & Rasplus, J.Y.R. (2012). Taxonomic revision and molecular phylogeny of the fig wasp genus *Anidarnes* Bouček, 1993 (Hymenoptera: Sycophaginae). *Systematic Entomology*.

Appendix S1. *Anidarnes* Bouček, 1993. Species re-descriptions. And non-type materials

Abbreviations for measurements used in the text include: POL, distance between posterior ocelli; OL, distance between posterior and anterior ocelli (measured from posterior ocellus to anterior ocellus); OOL, distance between posterior ocellus and eye margin

***Anidarnes bicolor* (Ashmead, 1900)**
(Figs 2A, 3A, 4A, 5A, 6A, 7A)

Material analyzed. 7♀ 7♂ USA, Florida, Miami, ex *F. aurea*, 2.5.1992, JY Rasplus leg. 4♀ USA, Coral Gables, ex *F. aurea*, 4.2.1993; 22♀ 18♂ USA, Florida Florida City (25.420393° -80.534593°), ex *F. aurea*, n° JRAS2874, A. Cruaud & JY Rasplus leg ; 3♀ 3♂ USA, Florida, Miami, Campus University (25.72° -80.28°), 09.1994, ex *F. aurea* n° JRAS1155, M. Hossaert-McKey leg.; 18♀ 4♂ USA, Florida, Florida City (25.460842° -80.486458°), 29.04.2010, ex *F. aurea*, n° JRAS2871-02, A. Cruaud & JY Rasplus leg (CBGP).

Diagnosis. Predominantly yellow brown. Vertex dark brown, black near ocelli. Metasoma darker. Malar sulcus absent. Median groove on vertex shallow, conspicuous near occipital foramen. Metascutellum trapezoidal (Fig. 6A), with a small median tooth on posterior margin. Supraclypeal area mostly smooth (Fig. 3A). Propodeal spiracle contiguous to metanotum (Fig. 6A). Metasoma entirely brown-black. Ovipositor longer than hind tibia, with median constriction.

Female. Body length 1.7–2.6mm. Ovipositor length 0.6mm. Predominantly yellow brown. Scape yellow, dorsal margin slightly brown. Pedicel and funicle brown. Vertex dark brown, black near ocelli. Pronotum yellow. Frenum dark brown. Legs brown yellow. Foretibia and tarsi yellow-white. Wings hyaline. Metasoma dark brown to black.

Head. Face reticulate. Pilosity short and sparse. Clypeus 1.5x as broad as high. Malar sulcus absent. Epistomal groove shallow. Supraclypeal area broad, wider than 0.5x torulus diameter, predominantly smooth. Subantennal groove shallow and smooth. Interantennal projection lanceolate and short, exceeding the torulus by less than 1x torulus diameter. Distance from torulus to median ocellus 0.2x distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.8x pedicel length. Funicle with two anelli. First funicular segment 0.7–0.8x as long as wide. 12th flagellomere (=terminal button) quadrate. POL 4.3–5.3x OOL. Vertex slightly concave. Median groove on vertex shallow, conspicuous near occipital foramen.

Mesosoma. Mesoscutum reticulated. Notauli faintly crenulate. Mesoscutal lateral lobe homogeneously reticulate. mesoscutellum 1.2–1.3x as long as wide. With engraved sculpture. Frenal sulcus densely crenulate. Frenum length ca. 0.7x metascutellum length. Metascutellum trapezoidal, with small median apical projection, medially reticulate, laterally striate, without basal crenulation. Propodeal median line present as an impressed line. Propodeal spiracle not separated from hind margin of metanotum. Wings with short and sparse pilosity. Postmarginal vein absent.

Metasoma. Mucro (hypopygial projection) short and broad. Ovipositor with median constriction. Ovipositor length 1.4x hind tibia length.

Relative measurements. See appendix S2.

Male. Similar to female, body and legs with extensive yellow coloration. Flagellomeres slightly longer than in females. 12th flagellomere elongate. Wings with long and dense pilosity.

Host plant. *Ficus aurea* Nuttall.

***Anidarnes brevicauda* Bouček, 1993**

(Figs 2B, 3B, 4B, 5B, 6B, 7B)

Diagnosis. Predominantly brown. Face yellow brown. Pronotum yellow. Lateral lobe of mesoscutum and axilla with yellow region. Legs brown, tarsi and foretibia yellow. Scutellum and anterior half of mesonotum smooth (Fig. 5B). Mesoscutum lateral lobe reticulate, becoming smooth near notaulus (Fig. 6B). Anterior half of mesoscutum mostly smooth (Figs 6B). Propodeal median line present as an impressed line.

Ovipositor as long as or shorter than hind tibia, with median constriction.

Female. Body length 2.5mm. Ovipositor length 0.5mm. Predominantly brown. Scape yellow, brown in dorsal margin. Pedicel yellow brown. Funicle brown. Face yellow brown. Pronotum yellow. Lateral lobe of mesoscutum and axilla with yellow region. Wings hyaline. Frenum dark brown. Legs brown, tarsi and foretibia yellow. Metasoma dark brown to black.

Head. Face reticulate. Pilosity short and sparse. Clypeus 0.9x as broad as high. Malar sulcus absent. Epistomal groove shallow. Supraclypeal area broad, wider than 0.5x torulus diameter, predominantly smooth. Subantennal groove shallow and smooth. Interantennal projection lanceolate and short, exceeding the torulus by less than 1x torulus diameter. Distance from torulus to median ocellus 0.2x distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.8–3x pedicel length. Funicle with two anelli. First funicular segment 0.8x as long as wide. 12th flagellomere elongate. POL 6.8x OOL. Vertex clearly concave. Median groove on vertex shallow, conspicuous near occipital foramen.

Mesosoma. Anterior half of mesoscutum smooth. Posterior half of mesoscutum reticulated. Notauli densely crenulate. Mesoscutal lateral lobe reticulate, becoming smooth near notaulus. mesoscutellum 1.4x as long as wide, with smooth sculpture. Frenal sulcus faintly crenulate. Frenum length ca. 1x metascutellum length. Metascutellum rectangular, striate, without basal crenulation. Propodeal median line present as an impressed line. Propodeal spiracle separated from the hind margin of metanotum by less than its own diameter. Wings with short and sparse pilosity. Postmarginal vein absent.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 0.9x hind tibia length.

Relative measurements. See appendix S2.

Male. Not known.

Host plant. *Ficus costaricana* (Liebmann)Miquel.

***Anidarnes globiceps* (Mayr)**

(Figs 2E, 3E, 4E, 5E, 6E, 7E)

***Anidarnes globiceps* (Mayr)**

Diagnosis. Predominantly yellow orange. Metasoma dorsally brown. Face smooth. Malar sulcus present (Fig 2E). Median groove on vertex conspicuous (Fig. 5E). Mesoscutum smooth. Metascutellum unconspicuous, poorly delimitated (Figs 5E & 6E). Ovipositor sheaths as long as hind tibia. OOL as long as OL (Fig. 5E). Ovipositor with median constriction, as long as hind tibia.

Female. Body length 2mm. Ovipositor length 0.5mm. Predominantly yellow orange. Antenna yellow. Head slightly brown between torulus and compound eye. Tarsi yellow. Wings hyaline. Metasoma dorsally brown.

Head. Face smooth. Pilosity short and sparse. Clypeus 1.1x as broad as high. Malar sulcus present. Epistomal groove present, delimiting clypeus dorsally. Supraclypeal area broad, wider than 0.5x torulus diameter, predominantly smooth. Subantennal groove shallow and smooth. Interantennal projection lanceolate and short, exceeding the torulus by less than 1x torulus diameter. Distance from torulus to median ocellus 0.3x distance from torulus to oral margin. Distance between toruli smaller than torulus diameter. Scape length 2.9x pedicel length. Funicle with two anelli. First funicular segment 0.7x as long as wide. 12th flagellomere elongate. POL 1.5x OOL. Vertex slightly concave. Median groove on vertex conspicuous.

Mesosoma. Mesoscutum smooth. Notauli faintly crenulate. Mesoscutal lateral lobe reticulate, becoming smooth near notaulus. mesoscutellum 1.6x as long as wide with smooth sculpture. Frenal sulcus faintly crenulate. Metascutellum virtually absent. Propodeal median line present. Propodeal spiracle separated from the hind margin of metanotum by about its own diameter. Wings with short and sparse pilosity. Postmarginal vein absent.

Metasoma. Mucro short and broad. Ovipositor with median constriction. Ovipositor length 1x hind tibia length.

Relative measurements. See appendix S2.

Male. Similar to females, flagellomeres slightly longer than in females.

Host plant. *Ficus* sp.

Farache, F. H. A.; Cruaud, A; Genson, G. Pereira, R.A.S. & Rasplus, J.Y.R. (2012). Taxonomic revision and molecular phylogeny of the fig wasp genus *Anidarnes* Bouček, 1993 (Hymenoptera: Sycophaginae). *Systematic Entomology*.

Appendix S2. *Anidarnes* Bouček, 1993. Relative measurements.

Abbreviations for measurements used in the text include: HT, hind tibia length; OV, ovipositor sheath length; SC, scape length; PD, pedicel length; F1, length of the first funicular segment; HW, head width; HL, head length; HH, head height; POL, distance between posterior ocelli; OL, distance between posterior and anterior ocelli (measured from posterior ocellus to anterior ocellus); OOL, distance between posterior ocellus and eye margin; TO, distance between torulus and anterior ocellus; TC, distance between torulus and clypeal ventral margin; EH, eye height; EL, eye length; MA, malar space length; PN, pronotum length; MS, mesoscutum length; SL, mesoscutellum length; SW, mesoscutellum width; PP, propodeum length; MV, length of the marginal vein; ST, length of the stigmal vein.

***Anidarnes bicolor* (Ashmead, 1900)**

HT = 77. OV = 108. SC = 31. PD = 11. F1 = 9. HW = 101. HL = 57. HH = 60. POL = 35. OL = 19. OOL = 8. TO = 10. TC = 48. EH = 49. EL = 39. MA = 18. PN = 48. MS = 57. SL = 44. SW = 36. PP = 25. MV = 13. ST = 24.

***Anidarnes brevicauda* Bouček, 1993**

HT = 87. OV = 78. SC = 42. PD = 15. F1 = 11. HW = 19. HL = 68. HH = 79. POL = 41. OL = 19. OOL = 6. TO = 12. TC = 52. EH = 55. EL = 47. MA = 21. PN = 45. MS = 70. SL = 51. SW = 36. PP = 31. MV = 25. ST = 30.

***Anidarnes brevior* Farache & Rasplus sp.n.**

HT = 75. OV = 59. SC = 29. PD = 14. F1 = 10. HW = 88. HL = 58. HH = 73. POL = 32. OL = 15. OOL = 10. TO = 12. TC = 47. EH = 45. EL = 36. MA = 15. PN = 40. MS = 60. SL = 42. SW = 33. PP = 26. MV = 12. ST = 30.

***Anidarnes dissidens* Farache & Rasplus sp.n.**

HT = 110. OV = 125. SC = 55. PD = 13. F1 = 12. HW = 142. HL = 83. HH = 115. POL = 31. OL = 10. OOL = 14. TO = 35. TC = 63. EH = 45. EL = 40. MA = 34. PN

= 45. MS = 100. SL = 75. SW = 45. PP = 37. MV = 20. ST = 23.

***Anidarnes globiceps* (Mayr)**

HT = 82. OV = 80. SC = 35. PD = 12. F1 = 11. HW = 112. HL = 75. HH = 84. POL = 26. OL = 17. OOL = 17. TO = 15. TC = 54. EH = 51. EL = 46. MA = 15. PN = 45. MS = 68. SL = 56. SW = 34. PP = 30. MV = 18. ST = 23.

***Anidarnes gracilis* Farache & Rasplus sp.n.**

HT = 108. OV = 150. SC = 39. PD = 15. F1 = 13. HW = 132. HL = 80. HH = 99. POL = 40. OL = 18. OOL = 12. TO = 22. TC = 61. EH = 65. EL = 53. MA = 23. PN = 34. MS = 70. SL = 68. SW = 37. PP = 41. MV = 15. ST = 26.

***Anidarnes isophlebiae* Farache & Rasplus sp.n.**

HT = 99. OV = 145. SC = 40. PD = 14. F1 = 12. HW = 128. HL = 79. HH = 98. POL = 37. OL = 20. OOL = 10. TO = 17. TC = 62. EH = 64. EL = 51. MA = 22. PN = 45. MS = 79. SL = 50. SW = 38. PP = 42. MV = 30. ST = 22.

***Anidarnes jimeneziae* Farache & Rasplus sp.n.**

HT = 70. OV = 73. SC = 29. PD = 11. F1 = 10. HW = 92. HL = 55. HH = 72. POL = 34. OL = 16. OOL = 8. TO = 11. TC = 47. EH = 44. EL = 34. MA = 16. PN = 40. MS = 56. SL = 39. SW = 32. PP = 30. MV = 14. ST = 19.

***Anidarnes longiscutellum* Farache & Rasplus sp.n.**

HT = 111. OV = 122. SC = 42. PD = 16. F1 = 12. HW = 134. HL = 82. HH = 108. POL = 41. OL = 20. OOL = 16. TO = 20. TC = 58. EH = 60. EL = 49. MA = 23. PN = 45. MS = 89. SL = 71. SW = 43. PP = 32. MV = 23. ST = 31.

***Anidarnes martinae* Farache & Rasplus sp.n.**

HT = 84. OV = 30. SC = 35. PD = 12. F1 = 9. HW = 119. HL = 62. HH = 84. POL = 35. OL = 18. OOL = 9. TO = 17. TC = 50. EH = 54. EL = 44. MA = 24. PN = 30. MS = 58. SL = 43. SW = 34. PP = 25. MV = 17. ST = 25.

***Anidarnes niger* Farache & Rasplus sp.n.**

HT = 74. OV = 89. SC = 28. PD = 15. F1 = 8. HW = 85. HL = 58. HH = 66. POL =

31. OL = 13. OOL = 8. TO = 19. TC = 46. EH = 42. EL = 33. MA = 13. PN = 31. MS = 53. SL = 41. SW = 28. PP = 25. MV = 15. ST = 33.

Anidarnes rugosus **Farache & Rasplus sp.n.**

HT = 103. OV = 85. SC = 47. PD = 16. F1 = 9. HW = 137. HL = 75. HH = 91. POL = 42. OL = 23. OOL = 12. TO = 23. TC = 53. EH = 58. EL = 47. MA = 21. PN = 37. MS = 67. SL = 55. SW = 42. PP = 33. MV = 11. ST = 26.