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A second New World hoverfly, *Toxomerus floralis* (Fabricius) (Diptera: Syrphidae), recorded from the Old World, with description of larval pollen-feeding ecology

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Abstract

Recently (2013–2014), several hoverfly specimens from two localities in Benin and Cameroon (West and Central Africa) were caught from a species that we could not identify using existing identification keys for Afrotropical Syrphidae. Specific identification as *Toxomerus floralis* (Fabricius) was accomplished using morphology and various Neotropical identification keys. Corroboration of this identification was made by sequencing of the standard COI barcode region and a subsequent BLAST-IDS in BOLD that revealed a 100% sequence similarity with *Toxomerus floralis* from Suriname (South America). Species identification was further supported by sequencing parts of the nuclear 18S and 28S rRNA genes. The species is widespread in Togo, Benin, Nigeria and Cameroon, and eggs, larvae and adults are abundant at several localities. Yet, the full extent of its geographic distribution within tropical Africa remains to be determined. This is only the second known established introduction of a non-African hoverfly species in the Afrotropics. Interestingly, the larvae of the species have been reported as predators of Aphididae and Delphacidae but we found them to be pollenivorous, which is a rare feeding mode within the subfamily Syrphinae. Moreover, it is the only known Syrphinae species of which the larvae feed on pollen from two plant species from different families (Cyperaceae and Orobranchaceae). This example illustrates how DNA barcoding may allow a fast and accurate identification of introduced species.

Key words: 18S rRNA, 28S rRNA, Afrotropics, Central Africa, West Africa, COI, DNA barcoding, flower fly, pollenivory

Introduction

Flower flies, or hoverflies (Insecta: Diptera: Syrphidae), are a species-rich family of insects that are amongst the most important flower pollinators (Proctor *et al.* 1996). Worldwide, there are *ca*. 6,000 species, divided into four subfamilies: Eristalinae, Microdontinae, Pipizinae and Syrphinae (Thompson 2013; Mengual *et al*. 2015). Syrphinae have until recently been considered to consist almost exclusively of species with terrestrial, predatory larvae, mostly preying upon Hemiptera: Aphidoidea (Rotheray 1993; Thompson & Rotheray 1998). Exceptionally, larvae have different life histories.

Subaquatic larvae of some *Ocyptamus* Macquart species are predatory on a wide range of Coleoptera and Diptera larvae in the phytotelmata of bromeliads (Bromeliaceae) in South America (Rotheray *et al*. 2000). At least three *Allograpta* Osten Sacken species from the highlands of Costa Rica have phytophagous larvae, namely,

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A. centropogonis Nishida, Rotheray & Thompson and *A. zumbadoi* Thompson, that are leaf-miners of *Centropogon* spp. (Campanulaceae) (Nishida *et al*. 2002; van Zuijen & Nishida 2010), and larvae of *A. micrura* Osten Sacken that feed on pollen of *Castilleja talamancensis* (Orobranchaceae) (Weng & Rotheray 2009). Larvae of the widespread New World species *Toxomerus politus* (Say) feed on pollen of maize (*Zea mays*) (Poaceae) (Marin 1969; Richardson 1915) and sorghum, *Sorghum bicolor* (Poaceae) in production fields in Brazil (Nunes-Silva *et al*. 2010), and larvae of *T. apegiensis* (Harbach) feed on pollen of *Olyra obliquifolia* (Poaceae) (Reemer & Rotheray 2009).

The genus *Toxomerus* is one of the most speciose genera of Syrphidae and currently comprises more than 150 species globally. The genus is confined to the New World (southern Canada to southern Chile and Argentina), but species richness is greatest in tropical regions (Thompson & Thompson 2006; Borges & Couri 2009). The introduction of the New World hoverfly species *Toxomerus floralis* (Fabricius) into West and Central Africa is reported here. The native distribution of *T. floralis* ranges from the USA (Texas and Florida) to southern South America (Thompson & Thompson 2007; Borges & Couri 2009; Thompson 2013). The records noted here for *T. floralis* in the Afrotropical Region are apparently only the second known introduction of a hoverfly from the New World into Africa. So far, only *Ornidia obesa* (Fabricius) is known to have spread from the New World into the Old World tropics (Macquart 1850; Thompson 1991). The larvae of this latter species feed on different types of semi-liquid, synanthropic material (*e.g*., animal dung, faeces, sewage, rotten fruits and vegetables) and also on animal carcasses (Martins *et al*. 2010).

Material and methods

Material. Initial records of the occurrence of *Toxomerus floralis* in the Afrotropical Region are based on 7 specimens (4♂, 3♀) from the Atlantique Province, Benin in West Africa (Fig. 1), at the International Institute of Tropical Agriculture in Calavi (IITA, Cotonou, latitude (decimal minutes): 06°25.191′N - longitude: 02°19.702′E), by G. Goergen, using an insect net (Table 1, Fig. 2). These specimens were preserved in 100% ethanol. Additional material from the Northwest Region, (Cameroon) that shared a similar morphology was examined in the collections of the National Museum, Bloemfontein (BMSA) (South Africa), comprising 12 pinned specimens (7♂, 5♀), swept from grasses and other vegetation on 2 June 2014 in the grounds of Université de Dschang (05°26.761′N, 10°04.237′E), in the Menoua District, Cameroon by A.H. Kirk-Spriggs (Table 1, Fig. 2).

Initially the specimens could not be identified using current available identification keys to Afrotropical Syrphidae, but were eventually identified as the genus *Toxomerus* using the identification key provided by Thompson (1999). Thereafter, keys to *Toxomerus* by Borges & Couri (2009), Curran (1930), Hull (1943), Metz & Thompson (2001) and Thompson (1981, 1999), were referred to, in order to identify the material to specific level. Thompson (1999) provides a glossary of taxonomic terms and this terminology is applied here. Material referred to in this study and voucher specimens are deposited at the National Museum, Bloemfontein (South Africa) (vouchers BMSA(D)53436 = 109D07, BMSA(D)53445 = 109D08, BMSA(D)53442 = 109E01, BMSA(D)53438 = 109E02) and the Royal Museum for Central Africa, Tervuren, Belgium (RMCA) (vouchers 107F01, 107F02, 107F04, 107F06, and 107F07). Additional specimens are in the collections of the International Institute of Tropical Agriculture, Cotonou, Benin (IITA).

Molecular analysis. Information on the specimens included in the molecular analysis is provided in Table 1. DNA was extracted from single hind legs of nine specimens (five from Calavi, Benin and four from Dschang, Cameroon) (Table 1), using a NucleoSpin Tissue Kit (Macherey-Nagel, Düren), following the manufacturer's instructions. PCR reactions were undertaken in 25 µl reaction volumes, that contained 1.5 mM $MgCl_2$ in 1x PCR buffer (Invitrogen), 0.2 mM of each dNTP, 0.2 µM of each primer and 0.5 units of Taq polymerase (Invitrogen). One mitochondrial and two nuclear gene fragments were sequenced. The DNA barcode fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified using primer pair LCO1490 and HCO2198 (Folmer *et al*. 1994). Parts of the ribosomal nuclear 18S and 28S rRNA were amplified using primer pairs 18S-SYR-1F (GGGAGCCTGAGAAACGGCTACC) and 18S-SYR-2R (CGAACCTCTAACTTTCGTTC), and 28S-SYR-1F (GGAACCAGCTACTAGATGGTTCG) and 28S-SYR-2R (GCGAAAAGAAATCAGTTCAGC), respectively (Scott Kelso & Jeff Skevington, personal communication).

TABLE 1. Geographic information on localities were *Toxomerus floralis* was sampled (decimal degrees and minutes) and a brief habitat description. *Mitracarpus hirtus* and/or *Cyperus rotundus* were found at all listed localities. Locality numbers are given in parenthesis and refer to the numbers on Fig. 1.

Country	Locality	Latitude	Longitude	Date	Habitat
Benin	Bohicon (1)	07°11.518′N	02°04.144′E	19/09/2014	free plot in town center
	Calavi IITA (2)	06°25.191′N	02°19.702′E	10/10/2014	wild vegetation in fallow plot
	Dassa-Zoumé (3)	07°46.917′N	02°10.944′E	19/09/2014	lawn area on hotel ground
	Parakou (4)	09°19.787′N	02°04.144′E	19/09/2014	vegetable gardens
	Porto Novo (5)	06°28.404′N	02°36.960′E	31/01/2015	botanical garden
Cameroon	Buea range (6)	04°07.264′N	09°18.446′E	18/10/2014	disturbed vegetation on cleared land
	Douala (7)	04°02.377′N	09°41.258′E	19/10/2014	free plot in town center
	Dschang (University) (8)	05°26.761′N	10°04.237′E	02/06/2014	cultivated plots and banana groves
	Sincoa (9)	05°45.119′N	10°09.589′E	13/12/2013	grasses and disturbed vegetation
Nigeria	Badagri, 4 km E of (10)	05°26.761′N	10°04.237′E	16/04/2015	fallow vegetation near highway
	Ibadan IITA (11)	07°29.717′N	03°53.807′E	11/04/2015	vegetation close to lake shore line
Togo	Lomé (12)	06°11.360′N	01°09.658′E	19/05/2015	vegetation around a temporary pond
	Kloto (13)	06°25.215′N	02°19.686′E	18/05/2015	cleared land in mid altitude
	Dzogbégan (14)	07°14.427′N	00°41.672′E	18/05/2015	grassland on monastery grounds

The PCR profile was an initial denaturation step of 5 min at 95 °C, followed by 35 cycles of 45 s at 95 °C, 45 s at an annealing temperature of 45 °C (COI) or 50 °C (18S and 28S) and 1.5 min at 72 °C, and ending with a final extension step of 5 min at 72 °C. PCR products were purified using the GFX PCR DNA Purification Kit (GE Healthcare) following the manufacturer's instructions. Purified DNA was diluted in 15 µl of sterile water. PCR-products were bidirectionally sequenced using the ABI PRISM BigDye ® Terminator v3.1 Cycle Sequencing Kit and run on an ABI3130xl Genetic Analyzer. Sequences were assembled in SeqScape v2.5 (Life Technologies) and inconsistencies were checked by eye on the chromatogram. Sequences were submitted to GenBank under accession numbers KR632611–KR632619 for COI, KR632594–KR632601 for 18S, and KR632602–KR632610 for 28S. These datasets were supplemented with DNA sequences from BOLD (for COI) and GenBank (for 18S and 28S), including *Ocyptamus dimidiatus* (Fabricius) (COI: EU409129; 18S: EU409239; 28S: EU409184) as outgroup. Sequences were aligned in MAFFT v7 (Katoh & Standley 2013) with default settings and needed no manual adjustments.

For COI, we obtained a sequence length of 591 bp, but since many *Toxomerus* sequences from BOLD/GenBank lacked part of the 3'-end, the dataset was trimmed to 537 bp, to include as many *Toxomerus* spp. and specimens as possible. Yet, several sequences of *T. marginatus* (Say) and *T. geminatus* (Say) even lacked larger parts at either the 3'- and/or 5'-end and were not included as there remained plenty of other representatives of both species with the entire 537 bp fragment. The final COI dataset thus comprised 512 *Toxomerus* sequences of 537 bp. COI sequences were translated to amino acid sequences to check for stop codons, but none were found. For the 18S and 28S rRNA gene fragments, the trimmed dataset comprised 352 bp (45 *Toxomerus* sequences) and 588 bp (51 *Toxomerus* sequences), respectively (data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.tm680).

Neighbour-Joining (NJ) trees (Saitou & Nei 1987) were constructed for each gene fragment, using the Kimura 2 parameter (K2P) model in MEGA v6 (Tamura *et al*. 2013), with pairwise deletion of missing data including insertions and deletions (indels). Unique sequences were selected in DAMBE v5 (Xia 2013). Branch support was evaluated with 1000 bootstrap replicates (Felsenstein 1985). Only bootstrap values ≥ 70% were considered as indicating strong support (Hillis & Bull 1993).

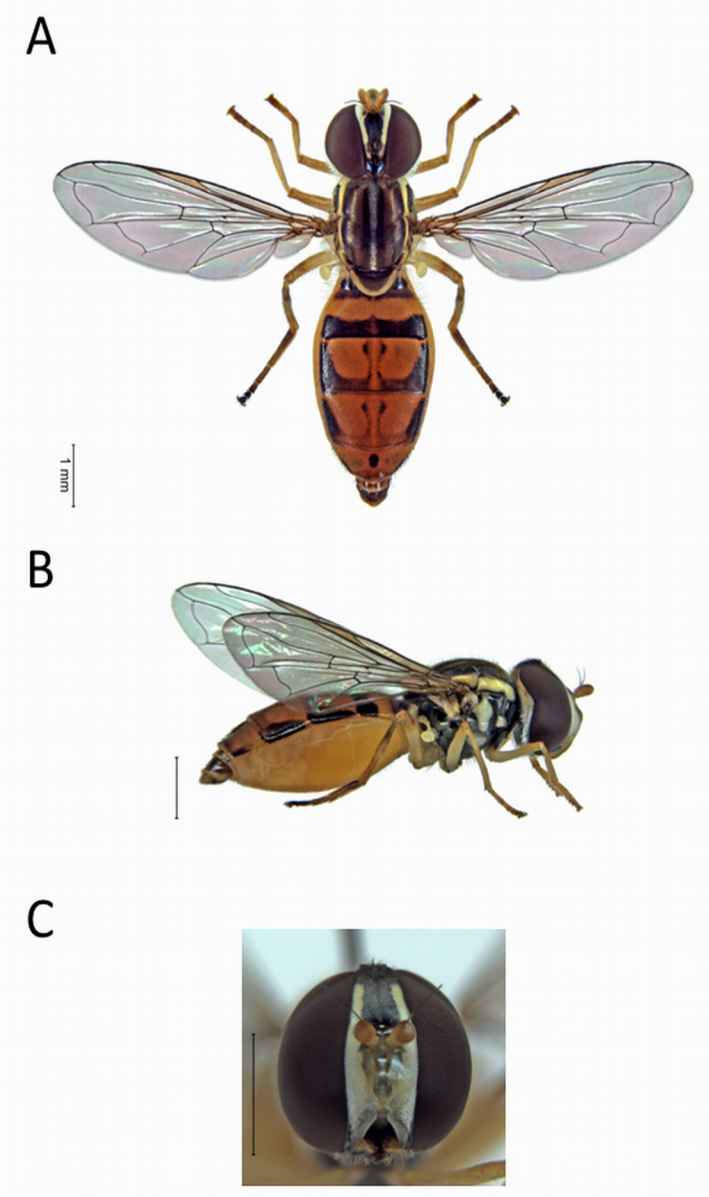

FIGURE. 1. Adult female *Toxomerus floralis* from Calavi (Benin). A. dorsal view; B. lateral view; C. frontal view of head. Scale bar = 1 mm. All pictures taken by G. Goergen.

Behaviour and host associations. In order to assess the distribution of *T. floralis* in West and Central Africa, several field surveys were undertaken in Togo (one survey), Benin (three surveys), Cameroon (three surveys) and Nigeria (two surveys) (Table 1, Fig. 2), during which vegetation and inflorescences were actively searched for the presence of *Toxomerus* adults. Adult specimens were sampled using an insect net and were stored in 100% ethanol. Identifications were verified upon return to the laboratory.

At the IITA station in Calavi (Benin), egg laying behaviour was observed in the field and vegetation was examined for the presence of eggs, larvae, and pupae of *T. floralis*. Located larvae and pupae were returned to the laboratory, where they were reared in Petri dishes. Following eclosion, adults were stored in 100% ethanol and were identified based on external morphology.

A qualitative study was also undertaken in order to study the feeding and oviposition behaviour of *T. floralis*, for which bunches of *ca.* 15–20 stalks of young, ear-producing *Cyperus rotundus* (Cyperaceae) were potted outdoors and enclosed in fine mesh netting. In each of the three successively tested enclosures *ca.* ten females were released and their behaviour studied.

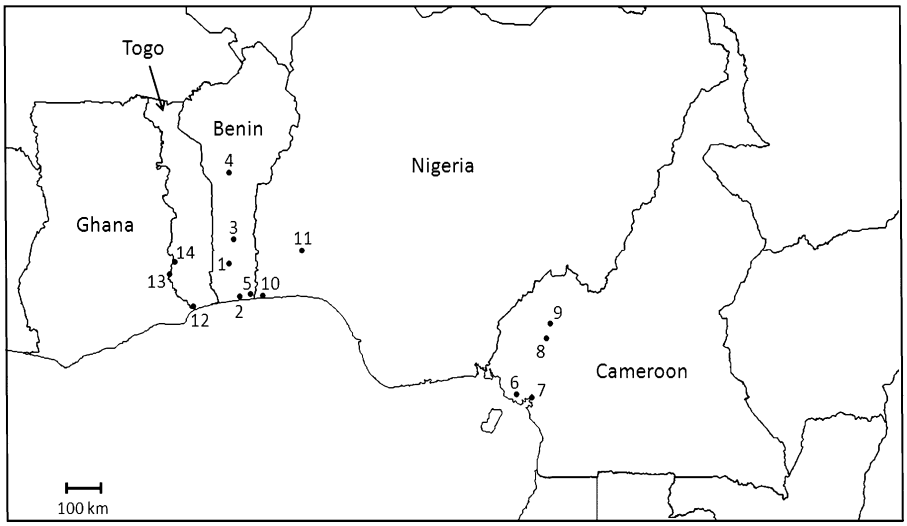

FIGURE 2. Map of West and Central Africa showing the localities where *Toxomerus floralis* was recorded in high numbers. Numbers on the map refer to the localities listed in Table 1.

Results and discussion

Morphology. Studied material was identified as belonging to the New World genus *Toxomerus* Macquart, characterised as follows: 1) postpronotum bare; 2) anterior anepisternum with distinct pilosity posterodorsally; 3) eye and metasternum bare; and 4) posterior margin of eye with distinct triangular emargination at level of insertion of antenna (Thompson 1999, Fig. 1A–C).

Using the identification keys to *Toxomerus* (listed above) the specimens were identified as *T. floralis* (Fabricius), characterised as follows: 1) small species (< 9 mm), with yellow face in male, face dark medially in female; 2) face *ca.* 1/3 as long as compound eye; 3) mesonotum with lateral yellow vitta extending from postpronotum to scutellum, the latter with whitish yellow pilosity; 4) entire anepimeron black; and 5) yellow supraprocoxal maculae present. Males are holoptic, have a short, but distinct postanal process (unlike *T. schlingeri* Thompson & Thompson, in which males are dichoptic and lack a postanal process) and the dorsal surface of the antennal surstylus has short setulae (Thompson 1999, Fig. 14) (unlike *T. mosaicus* Borges & Couri, in which the dorsal surface of the antennal surstylus has long setulae in the apical 2/3; this species also possesses a yellow dorsal part of the anepimeron). The pattern of vittae on the male and female abdomen is variable. Figures are provided by Thompson & Thompson (2006, Fig. 8 for the male, Fig. 9 for the female) and in Fig. 1 of this study for the female.

Molecular analysis. The nine specimens sequenced had the same COI haplotype as the single *T. floralis* specimen in BOLD/GenBank [GBSYR049-10; EU409157; voucher MZH_XP115 from Suriname (Mengual *et al*. 2012)] (K2P-distance = 0; Fig. 3). Similarly, the nine 28S rRNA sequences of *T. floralis* were of a single haplotype and similar to the *T. floralis* sequence EU409211 from Suriname (Mengual *et al*. 2012) that was present in GenBank (K2P-distance = 0; Fig. 4). The 18S rRNA data did not indicate substantial variation within *Toxomerus*, with only four haplotypes across the entire genus. The *T. floralis* specimens belonged to a single haplotype that was shared with 18 other *Toxomerus* species (K2P-distance = 0; NJ-tree not shown), including a *T. floralis* sequence EU409288 from Suriname (Mengual *et al*. 2012).

Behaviour and host associations. *Toxomerus floralis* was located at several localities between Kloto (Togo) and Buea (Mt Cameroon range, NW Cameroon) and to the north, as far as the dry savanna at Parakou (Central Benin, approximately 500 km N of Cotonou) (Table 1, Fig. 2), a straight distance of approximately 1,300 km. The relatively wide distribution range of this species, its presence in different habitats (ranging from mesic and xeric savanna to Afromontane), its high numbers and presence of eggs (Fig. 5A), larvae (Fig. 5B and 5C) and pupae (Fig. 5D) at several localities, indicate that the species is well-established in the studied areas.

At the IITA station Calavi (Benin), caged females were observed ovipositing on inflorescence of *Cyperus rotundus* (commonly termed nut-grass, coco-grass, purple nut sedge, red nut sedge, or Java grass). Larvae and

pupae were also recorded in the field on *C. rotundus*, and the numerous pupae that were collected all produced adult *T. floralis*, in total absence of any Aphidoidea. Hence, *C. rotundus* can be considered a host-plant of *T. floralis*. *Cyperus rotundus* is native and widespread in the Afrotropics (IUCN 2015) . This plant species has been considered the World's worst weed (Holm *et al*. 1977) and has been introduced into many parts of the world, including the native distribution range of *T. floralis*.

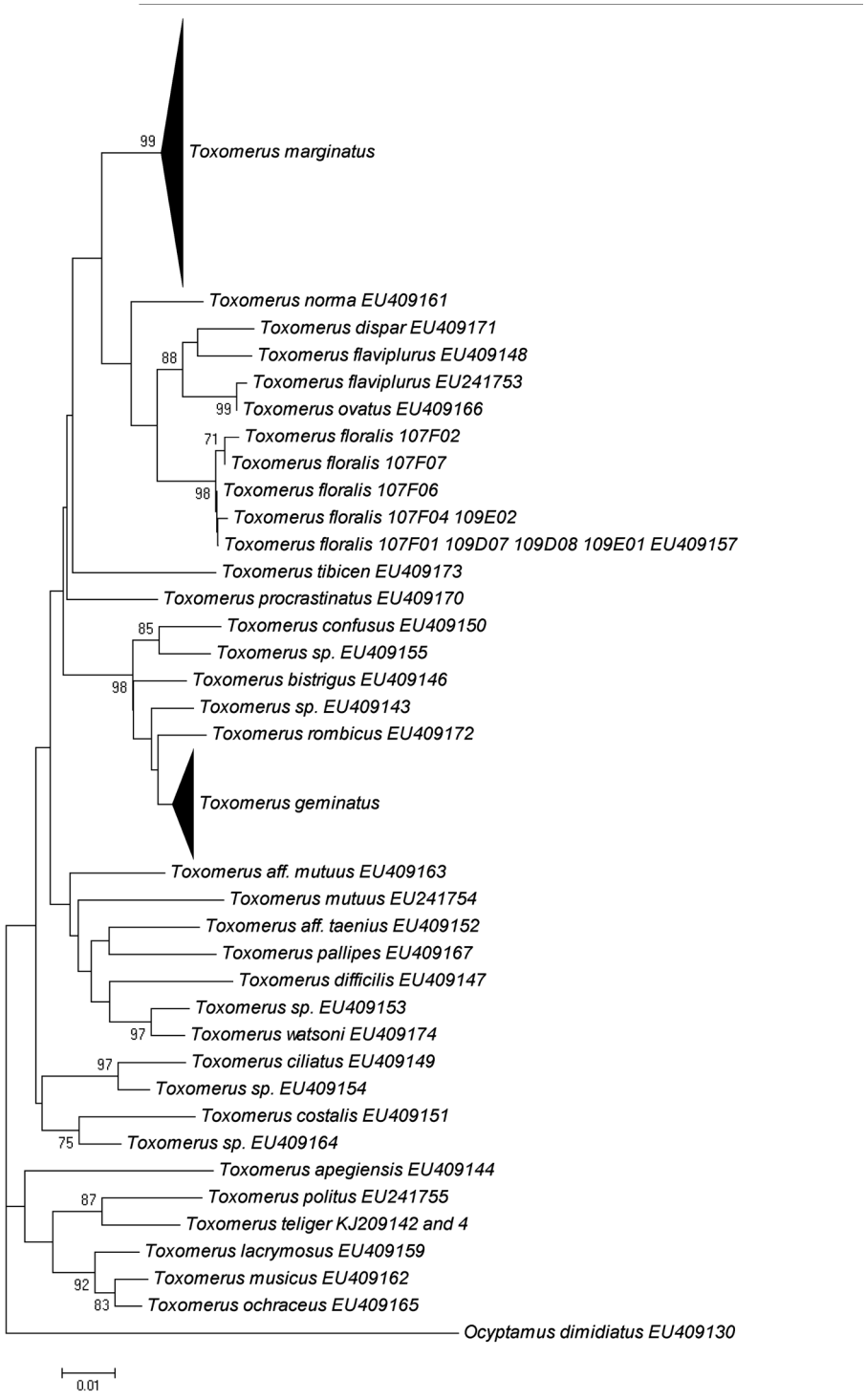

FIGURE 3. Neighbor-Joining tree of a 537 bp alignment of the mitochondrial cytochrome *c* oxidase subunit I gene (COI). Bootstrap values ≥ 70% are shown at the nodes. The scale bar indicates 0.01 substitutions per amino acid position.

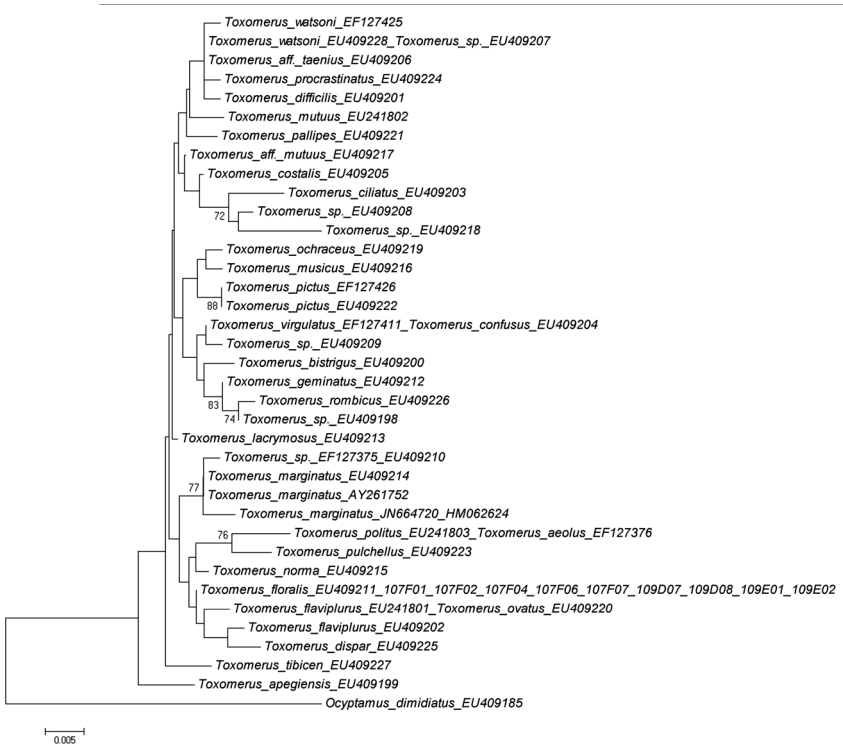

FIGURE 4. Neighbor-Joining tree of a 588 bp alignment of the nuclear ribosomal 28S rRNA gene. Bootstrap values ≥ 70% are shown at the nodes. The scale bar indicates 0.01 substitutions per amino acid position.

Several larvae and pupae that were potentially of *T. floralis* were found on *Mitracarpus hirtus* (= *M. villosus*; see Nicholson (1977) for a discussion on the nomenclature; commonly termed tropical girdlepod or small squareweed) (Rubiaceae) (Fig. 5C). *Mitracarpus hirtus* is native to the New World and occurs from northern Mexico to southern South America (IUCN 2015)). It is unknown when this plant species was introduced into Africa, but today the species is widespread in tropical Africa (IUCN 2015), where it is well known for its analgesic and anti-inflammatory properties (*e.g.*, Onawumi Oluwayemi *et al*. 2012). Full grown larvae found on *M. hirtus* were returned to the laboratory, where they were allowed to pupariate. Adults (n = 7) emerged 2–3 days later and were identified as *T. floralis.* Larvae reared on *M. hirtus* in the laboratory were frequently found on inflorescences, and were observed to be active for considerable periods with the head inserted in the inflorescence (Fig. 5C). Direct feeding was observed on the pollen of *M. hirtus* and examination of larval gut contents confirmed the presence of quantities of pollen after the larva had spent some time on an inflorescence. The larvae have a pair of fleshly lobes that contain the mandibles, that can be extended beyond the labrum/labium (Fig. 5B), as also found in *T. apegiensis* (Reemer & Rotheray 2009) and *A. micrura* (Weng & Rotheray 2009). This character is believed to be an adaptation towards pollenivory, but is absent in *T. politus* (Reemer & Rotheray 2009).

Observations indicate that both *C. rotundus* and *M. hirtus* are host-plants of *T. floralis* and thus that its larvae are polyphagous. We never observed the larvae feeding on aphids during field surveys. *Toxomerus floralis* appears to be the first known hoverfly with larvae that feed on pollen from plants of more than one botanical family. The widespread occurrence of *C. rotundus* and *M. hirtus*, both of which are known to endure poor environmental and climatic conditions, may have facilitated the introduction of *T. floralis*. The date of introduction remains unknown, as most regions of the Afrotropics have been inadequately sampled for Syrphidae. The absence of records of *T. floralis* in the literature on Afrotropical Syrphidae suggests that the introduction may be relatively recent, despite both host-plant species being widespread in the Afrotropics for a considerable period. However, *T. floralis* is a small, inconspicuous hoverfly that flies sluggishly through dense vegetation and may, therefore, have remained long unnoticed and under-collected.

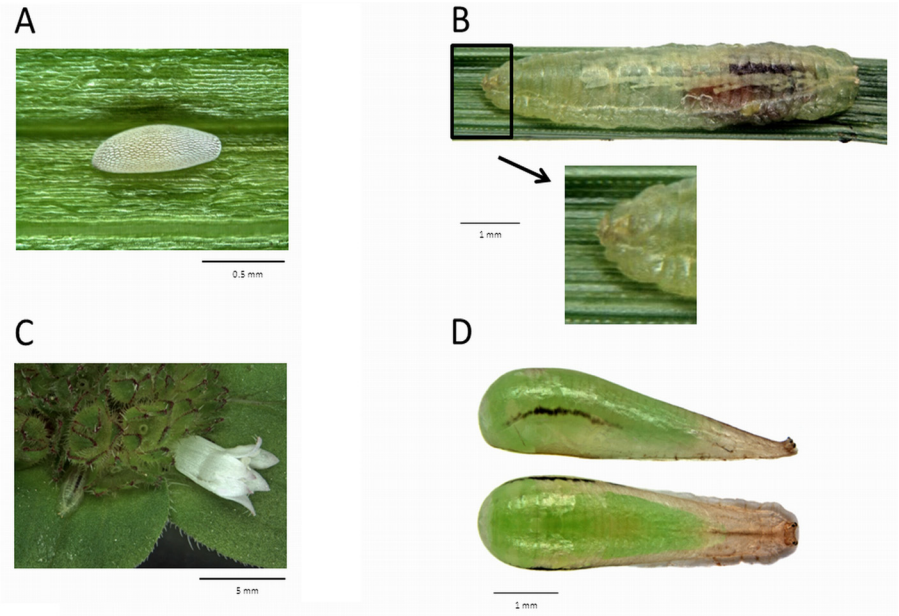

FIGURE 5. A. Egg of *T. floralis* on *Cyperus rotundus* (Calavi, Benin); B. Larva of *T. floralis* on *C. rotundus* (Calavi, Benin); the enlarged area shows the pair of lobes (that contain the mandibula) that extends beyond the head); C. Larva of *T. floralis* on *Mitrocarpus hirtus* (Calavi, Benin); D. Lateral (top) and dorsal (bottom) view of the puparium of *T. floralis* (Calavi, Benin). Scale bar = 0.5 mm for A; 1 mm for B and D and 5 mm for C. All pictures taken by G. Goergen.

Our observations on the pollenivorous feeding behaviour of the larvae of *T. floralis* are surprising. Indeed, Rojo *et al*. (2003) list the larvae of *T. floralis* as predators of aphids and nymphs of Delphacidae based on the findings by Loftin & Christenson (1933) and Wolcott (1948). Loftin & Christenson (1933) found, in Cuba, larvae of *T. floralis* [as *Mesogramma subannulata* Loew, but Curran (1925) considered *M. subannulata* a synonym of *Mesogramma floralis* Fabricius (= *T. floralis* (Fabricius)] feeding on the aphid *Rhopalosiphum maidis* (Fitch) (on *Zea mays*) and on nymphs of the delphacid *Peregrinus maidis* (Ashmead) (on *Sorghum*) whereas Wolcott (1948), in Puerto Rico, found the larvae (also as *M. subannulata*) feeding on the aphid *Sipha flava* (Forbes) and perhaps also on the aphid *Myzus persicae* (Sulzer) (on sugar cane *Saccharum officinarum* and *Capsicum* sp., respectively). However, it is not unlikely that Loftin & Christenson (1933) and Wolcott (1948) misidentified their specimens, and were referring to *Toxomerus dispar* (Fabricius). Indeed, *Toxomerus dispar* and *T. floralis* are both highly variable species and are the two most abundant *Toxomerus* species in the West Indies and Mesoamerica. As a result there has been considerable confusion as to the correct identity of these species and their associated names, and all published records of *M. subannulata* refer to either *T. dispar* or *T. floralis*, or both (see discussion in Thompson 1981). Thus, it could be that both Loftin & Christenson (1933) and Wolcott (1949) observed the feeding behaviour of the larvae of *T. dispar* , who's larvae have been reported to feed on aphids and caterpillars (Guagliumi 1962; Bartoszeck 1975). Unfortunately they neither provide details on the identification of the larvae nor on the morphology of the adult flies. Because 1) the morphology of our specimens corresponds to the description of *T. floralis*, 2) our COI and 28S rRNA sequences show a 100% similarity with those of *T. floralis* from Mengual *et al*. (2008), and 3) *T. floralis* and *T. dispar* differ at both COI and 28S rRNA (even though they are in the same clade) (Mengual *et al.* 2008), we believe that the identification of our specimens as *T. floralis* is correct. Alternatively, it could be that the larvae of *T. floralis* are opportunistic and are both predaceous and pollenivorous but this remains to be investigated as we did not observe larvae feeding on aphids in the Afrotropics.

Finally, to date, the larval feeding biology is known for only nine *Toxomerus* species, six of which (*T. boscii* Macquart, *T. corbis* (Walker), *T. dispar*, *T. geminatus*, *T. marginatus*, and *Toxomerus* sp.) are predators (Rojo *et al*. 2003) and three (*T. politus*, *T. apegiensis* and *T. floralis*) of which are phytophagous (see Introduction). A phylogenetic analysis of the tribe Toxomerini (Mengual *et al.* 2012), based on sequence data of three gene regions (COI, 18S rRNA, 28S rRNA), indicated that the phytophagous species *T. politus* and T. *apegiensis* belong to the same clade ('*politus*-group' *sensu* Mengual *et al*. 2012), together with six other species for which no larval information is available. Reemer & Rotheray (2009) suggested that the *politus*-group may represent a

phytophagous clade with pollenivorous larvae. *Toxomerus floralis* belongs to another clade ('*floralis*-group' *sensu* Mengual *et al*. 2012) containing (at least) five other species, of which *T. dispar* and *T. marginatus* are aphidophagous. As phylogenetic relationships among *Toxomerus* species-groups has not been adequately resolved (Mengual *et al*. 2008, 2012), no speculation can here be made as to the number of times pollen-feeding has evolved within *Toxomerus*, but it is likely, as in *Allograpta* (Mengual *et al*. 2008; van Zuijen & Nishida, 2010), to have evolved independently at least twice (Mengual *et al*. 2012; Reemer & Rotheray, 2009).

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References

Borges, Z.M. & Couri, M.S. (2009) Revision of *Toxomerus* Macquart, 1855 (Diptera: Syrphidae) from Brazil with synonymic notes, identification key to the species and description of three new species. *Zootaxa*, 2179, 1–72.

Curran, C.H. (1925) Some syrphid synonymy, (Diptera). *Canadian Entomologist*, 57, 307. http://dx.doi.org/10.4039/Ent57307a-12

Curran, C.H. (1930) New Diptera belonging to the genus *Mesogramma* Loew (Syrphidae). *American Museum Novitates*, 405, 1–14.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783–791. http://dx.doi.org/10.2307/2408678

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Holm, L., Plucknett, D., Pancho, J. & Herberger, J. (1977) *The world's worst weeds.* University of Hawaii Press, Honolulu, HI, 609 pp.

Hillis, D.M. & Bull, J.J. (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology*, 42, 182–192. http://dx.doi.org/10.1093/sysbio/42.2.182

Hull, F.M. (1943) The genus *Mesogramma. Entomológica Americana*, 23, 1–41.

IUCN (2015) The IUCN Red List of Threatened Species. Version 2015-3. Available from: http://www.iucnredlist.org (accessed 1 September 2015)

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30, 772–780. http://dx.doi.org/10.1093/molbev/mst010

Loftin, U.C. & Christenson, L.D. (1933) A report on the Corn Aphis, *Aphis maidis* Fitch, in Cuba. *Bulletin of the 4th Congress of the International Society of Sugar Cane Technology*, 115 (1932), 1–20.

Macquart, J.P.M. (1850) Diptères exotiques nouveaux ou peu connus. 4.e supplement. *Mémoires de la Société Royale des Sciences, de l'Agriculture et des Arts, de Lille, 1849*, 309–479, pls. 1–14. [reprinted with pagination of pp. 5–161, Roret, Paris. 1851.]

Marin, A.J.C. (1969) Nota sobre larvas de *Mesograpta polita* (Say) (Syrphidae, Diptera) en espigas de maiz (*Zea mays* L.) en El Limón, Aragua, Venezuela. *Agronomía tropical* (Venezuela), 19, 335–339.

Martins, E., Neves, J.A., Moretti, T.C., Godoy, W.A.C. & Thyssen, P.J. (2010) Breeding of *Ornidia obesa* (Diptera: Syrphidae: Eristalinae) on pig carcasses in Brazil. *Journal of Medical Entomology*, 47, 690–694. http://dx.doi.org/10.1093/jmedent/47.4.690

Mengual, X., Ståhls, G. & Rojo, S. (2008) Molecular phylogeny of *Allograpta* (Diptera, Syrphidae) reveals diversity of lineages and non-monophyly of phytophagous taxa. *Molecular Phylogenetics and Evolution*, 49, 715–727. http://dx.doi.org/10.1016/j.ympev.2008.09.011

Mengual, X., Ståhls, G. & Rojo, S. (2012) Is the mega-diverse genus *Ocyptamus* (Diptera, Syrphidae) monophyletic? Evidence from molecular characters including the secondary structure of 28S rRNA. *Molecular Phylogenetics and Evolution*, 62, 191–205.

http://dx.doi.org/10.1016/j.ympev.2011.09.014
Mengual, X., Ståhls, G. & Rojo, S. (2015) Phylogenetic relationships and taxonomic ranking of pipizine flower flies (Diptera: Syrphidae) with implications for the evolution of aphidophagy. *Cladistics*, 31 (5), 491–508. http://dx.doi.org/10.1111/cla.12105
Metz, M.A. & Thompson, F.C. (2001) A revision of the larger species of *Toxomerus* (Diptera: Syrphidae) with description of a new species. *Studia dipterologica*, 8, 225–256.
Nicolson, D.H. (1977) Typification of names *vs*. typification of taxa: proposals on Article 4 and reconsideration of *Mitracarpus hirtus* vs. *M. villosus* (Rubiaceae). *Taxon*, 26, 569–574. http://dx.doi.org/10.2307/1219653
Nishida, K., Rotheray, G. & Thompson, F.C. (2002) First non-predaceous syrphine flower fly (Diptera: Syrphidae): a new leaf-mining *Allograpta* from Costa Rica. *Studia dipterologica*, 9, 421–436.
Nunes-Silva, P., Cordeiro, G.D., Obregon, D., Neto, J.F.L., Thompson, C.F., Viana, B.F., Freitas, B.M. & Kevan, P.G. (2010) Pollenivory in larval and adult flower flies: pollen availability and visitation rate by *Toxomerus politus* Say (Diptera: Syrphidae) on sorghum *Sorghum bicolor* (L.) Moench (Poaceae). *Studia dipterologica*, 17, 177–185.
Onawumi Oluwayemi, O.E., Adelowo F.E., Ipadeola A.O., Edewor, T.I., Ayoola, P.B. & Odunola, O.A. (2012) Preliminary studies on phytochemical and antimicrobial investigation of plants (Irawo-Ile) *Mitracarpus villosus*, *Euphorbia hirta* and *Spermacoce ocymoides*. *International Journal of Research and Reviews in Applied Sciences*, 10, 78–81.
Proctor, M., Yeo, P. & Lack, A. (1996) *The Natural History of Pollination*. Harper Collins, London, 479 pp.
Reemer, M. & Rotheray, G.E. (2009) Pollen feeding larvae in the presumed predatory syrphine genus *Toxomerus* Macquart (Diptera, Syrphidae). *Journal of Natural History*, 43, 939–949. http://dx.doi.org/10.1080/00222930802610576
Richardson, C.H. (1915) A contribution to the life history of the corn-feeding *Syrphus* fly (*Mesogramma polita* Say). *Journal of Economic Entomology*, 8, 338–342. http://dx.doi.org/10.1093/jee/8.3.338
Rojo, S., Gilbert, F., Marcos-García, M.A., Nieto, J.M. & Mier Durante, M.P. (2003) *A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey.* CIBIO Ediciones, Alicante, 219 pp.
Rotheray, G.E. (1993) Colour guide to hoverfly larvae (Diptera, Syrphidae). *Dipterist's Digest*, 9, 1–156.
Rotheray, G.E., Zumbado, M., Hancock, E.G. & Thompson, F.C. (2000) Remarkable aquatic predators in the genus *Ocyptamus* (Diptera, Syrphidae). *Studia dipterologica*, 7, 385–398.
Saitou, N. & Nei, M. (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, 4, 406–425.
Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729. http://dx.doi.org/10.1093/molbev/mst197
Thompson, F.C. (1981) The flower flies of the West Indies (Diptera: Syrphidae). *Memoirs of the Entomological Society of Washington*, 9, 1–200.
Thompson, F.C. (1991) The flower fly genus *Ornidia* (Diptera: Syrphidae). *Proceedings of the Entomological Society of Washington*, 93, 248–261.
Thompson, F.C. (1999) A key to the genera of the flower flies (Diptera: Syrphidae) of the Neotropical Region including descriptions of new genera and species and a glossary of taxonomic terms. *Contributions on Entomology*, 3, 321–378.
Thompson, F.C. (2013) Family Syrphidae. *In*: Thompson, F.C. & Pape, T. (Eds.), *Systema Dipterorum. Version 1.5*. Available from http://www.diptera.org (accessed 1 September 2015)
Thompson, F.C. & Rotheray, G. (1998) 3.5. Family Syrphidae. *In*: Papp, L. & Darvas, B. (Eds.), *Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance) Vol. 3. Higher Brachycera*. Science Herald, Budapest, pp. 81–139.
Thompson, F.C. & Thompson, B.J. (2006) A new *Toxomerus* species from Chile (Diptera: Syrphidae). *Studia dipterologica*, 13, 317–331.
van Zuijen, W.W. & Nishida, K. (2010) Life history and immature stages of *Allograpta zumbadoi* Thompson, a phytophagous flower fly (Diptera: Syrphidae: Syrphinae). *Studia dipterologica*, 17, 37–51.
Weng, J.L. & Rotheray, G.E. (2008) Another non-predaceous syrphine flower fly (Diptera: Syrphidae): pollen feeding in the larva of *Allograpta micrura*. *Studia dipterologica*, 15, 245–258.
Wolcott, G.N. (1948) The Insects of Puerto Rico. *Journal of Agriculture of the University of Puerto Rico*, 32, 417–532.
Xia, X. (2013) DAMBE5: A comprehensive software package for data analysis in molecular biology and evolution. *Molecular Biology and Evolution*, 30, 1720–1728. http://dx.doi.org/10.1093/molbev/mst064